THE STRUCTURE AND FUNCTION OF WARM TEMPERATE ESTUARINE FISH COMMUNITIES

BY

JAMES K. SCHOOLEY

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Abstract of Dissertation Presented to the Graduate Council of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

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James K. Schooley

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The seagrass beds of Mosquito Lagoon and the nearby impounded marshes are the most northern portions of the Indian River and lie on the east central coast of Florida. A study of the seasonal fluctuations in water temperature, salinity, benthic invertebrate communities, and macrozooplankton standing crops was combined with estimates of annual detrital input to interpret differences in the structure and function of the fish communities in the impounded marshes and the open seagrass beds of the lagoon.

The two impounded marsh sites under study had salinity ranges of 10-28°/$_{oo}$ and 25-38°/$_{oo}$ during the period of this study. The ranges of water temperatures in the impoundments were 6-37°C and in the seagrass beds, 8-39°C during this study. Based on monthly fluctuations in salinity and temperature, it was concluded that the impoundments were no more physiologically stressful for resident fish than the seagrass beds.

Net detrital input to the shallow impoundment was 4,306 kilojoules·m^{-2}·$year^{-1}$, 75% of which came from black mangrove litter-fall. Net

detrital production by the seagrasses in the open lagoon sites was 2,413-3,707 $kJ \cdot m^{-2} \cdot y^{-1}$. The macrozooplankters most common to each site were calanoid copepods, caridean shrimp, and nematodes. Seagrass beds had higher densities of caridean shrimp and brachyuran larvae. The benthic infauna was dominated by bivalves in the impoundments and polychaetes in the seagrass beds. The absence of large decapods, especially blue crabs, and the limited fish fauna of the impoundments are suggested as reasons for the vastly different benthic communities found in the two habitats.

Structurally, the fish communities of the impoundments were dominated by several species of fishes in the order Atheriniformes. Most common were Cyprinodon variegatus, Poecilia latipinna, Gambusia affinis, Lucania parva, and Menidia peninsulae. The clown goby, Microgobius gulosus, was also consistently found. In the seagrass beds, the dominant resident community members were Lucania parva, Menidia peninsulae, Microgobius gulosus, Gobiosoma robustum, and Syngnathus scovelli. Significant seasonal recruits to the seagrass beds, primarily represented as juveniles, were Lagodon rhomboides and Bairdiella chrysoura.

Average fish densities in the impounded marsh were 16.5-27.5 (Ind/m^2) and in the seagrass beds, 3.6-7.3 (Ind/m^2). Average fish standing crops were 53.7-58.5 kJ/m^2 in the impoundments and 5.5-6.9 kJ/m^2 in the seagrass beds. Complexity of community structure was positively correlated with median water temperature at all sites. At only one of the two seagrass sites was there a significant positive correlation between community structure and seagrass density.

Functionally, the impoundment fishes were estimated to have consumed 992-1,059 $kJ \cdot m^{-2} \cdot y^{-1}$, respired 512-655 $kJ \cdot m^{-2} \cdot y^{-1}$ and had a net

production of 192-281 $kJ \cdot m^{-2} \cdot y^{-1}$. In contrast, the seagrass bed fishes are estimated to have consumed 91-118 $kJ \cdot m^{-2} \cdot y^{-1}$, respired 60-81 $kJ \cdot m^{-2} \cdot y^{-1}$, and had net fish productions of 13 $kJ \cdot m^{-2} \cdot y^{-1}$. The turnover rates of energy for the impoundment fishes were 3.6-5.2 per year, while the seagrass beds were 1.9-2.4 per year. The impoundment fishes appear to be more efficient at converting consumed energy into net fish production than the seagrass bed fishes. The efficiencies of other energy transfers, the influence of herbivore/detritivores, and fish generation times are discussed in comparing the two fish community types to each other and to other aquatic systems in general.

INTRODUCTION

Few researchers have attempted to assemble an ecosystem model for shallow estuarine systems. Notable attempts at structurally and functionally describing these complex systems in terms of energy flow are Day et al. (1973) for Barataria Bay in Louisiana, Odum et al. (1974) for Crystal River, Florida, and Thayer et al. (1975a) for the grass beds of the Newport River, North Carolina. Except for the Crystal River study, most models are the result of the synthesis of community and population studies, only some of which may have contemplated integration into an ecosystem model.

In attempting to synthesize previous studies into models, structural characteristics are often better understood than are functional characteristics of the various communities or populations within the ecosystem (Day et al. 1973). This is also usually the case for estuarine fishes. Even though a variety of structural references concerning species composition, seasonality, and, in some cases, density, is available for most larger estuarine systems, very little information on the energetic functioning of fishes is available. These functional characteristics would include estimates of respiration, production, and consumption. Excellent contributions to our understanding of the consumption process, and ultimately energetic functioning, include the Harringtons' (1961) food selection study of salt marsh fishes, Odum and Heald's (1972) trophic analysis of the North River estuary in south Florida, Carr and Adams' (1973) classic analysis of the ontogenetic

feeding changes of fishes in seagrass beds of west Florida, and Whitfield's (1980) work on the energy flow in a south African estuary. The work by Adams (1976a,b) on the fish communities in Zostera beds in the Newport River estuary, North Carolina, is an excellent example of a study that structurally and functionally describes a community and is later integrated into an ecosystem model (Ferguson and Adams 1979).

One estuarine system that only recently has come under intensive study is that of the Indian River on Florida's east central coast, the northern portion of which is shown in Figure 1. Gilmore (1977) has done a summary of the geography and hydrology of the Indian River in his review of the fish fauna of the region.

Prior to the mid-1950's, the high marshes within the Indian River were accessible to fishes of the open lagoon. However, since then, nearly all high marsh has been isolated from the lagoon by earthen dikes for mosquito control purposes (Provost 1969, 1973). On Merritt Island, this resulted in over 22 hectares of marsh being isolated, as well as partitioned by these dramatic management practices (Provost 1969, 1973). Snelson (1976) has done a preliminary survey of the fishes of the various impounded marsh habitats of northern Merritt Island. The impact of this impoundment on the entire estuarine fish community has never been evaluated. Without the experimental control of a similar large estuary with an unimpounded marsh such a determination would be difficult.

One aspect of fish community ecology that is testable within this modified system is the impact of this isolation on the populations of several species that are common to both the impoundments and seagrass beds (Snelson 1976, Gilmore 1977). These populations will serve as

Figure 1. The northern Indian River and sampling locations; ○ = impoundment 1 (I1), ● = impoundment 2 (I2), □ = seagrass bed 1 (S1), ■ = seagrass bed 2 (S2).

80°W
30°N
ATLANTIC OCEAN
PENSACOLA
JACKSONVILLE
TAMPA
MIAMI
GULF OF MEXICO
ATLANTIC OCEAN
MOSQUITO
LAGOON
HALIFAX
CANAL
BANANA CREEK
CAUSEWAY
INTRACOASTAL
TITUSVILLE
CAUSEWAY
INDIAN RIVER
WATERWAY
MERRITT
ISLAND
BANANA RIVER
CAPE
CANAVERAL
MOSQUITO
LAGOON
BIRD
ISLAND
PELICAN
ISLAND
EDDY CR
MAX HOECK CR

excellent ecological indicators of the relative differences in structure and function between fish communities in the impounded marsh and those in the seagrass beds.

The objectives of this study are

(1) to examine and compare the structure and energetic functioning of fish communities in impounded marsh and open seagrass beds;

(2) to elucidate relationships between the observed properties of the fish communities and abiotic and biotic factors;

(3) to characterize the functional aspects of the fish communities in terms of efficiencies of transfer in order to compare the systems studied to other aquatic systems in general;

(4) to provide information useful in developing ecosystems models of the impounded marsh and seagrass beds.

STUDY AREA

The northern Indian River and Mosquito Lagoon are shown in Figure 1. The term "river" is a misnomer. Indian River is a large, shallow, mesohaline lagoon that extends 250 kilometers along the east central coast. The lagoon is separated from the ocean by a barrier island that is cut in five places by artificial inlets. In the northern portion of the system this barrier island is at its widest and is known as Merritt Island. The Mosquito Lagoon is separated from the rest of the Indian River by a second strip of land. This land has been cut at the Haulover Canal to form a passageway for the intracoastal waterway. The closest access to the ocean from Mosquito Lagoon is through the Ponce de Leon Inlet, 80 kilometers north of Haulover Canal, just off the map shown in Figure 1.

The average water depth of Indian River is 1.5 m, with the maximum depths in areas dredged for channels, harbors, and land fill. The bottom of the lagoon is covered by extensive seagrass beds, dominated by Halodule wrightii and Syrinogodium filiforme. In the northern part of the system (Fig. 1), tidal fluctuations are insignificant; the major water movements are the result of wind-driven circulation (Dubbelday 1975). Lasater (1975) reported that in Mosquito Lagoon, salinity ranges from 21-36°/$_{oo}$, with a yearly average of 31.1°/$_{oo}$. Because of the lack of significant fresh water input, the salinity of the lagoon at any given time represents a balance between evaporation and local precipitation (Lasater 1975).

Two seagrass beds within the Mosquito Lagoon were studied. The first, S1, is located in Eddy Creek at the southern end of the lagoon, where water depth was approximately 0.5 m. The second seagrass site, S2, was located off of an area known as Van's Island, approximately 18 km from S1. Water depth at S2 was approximately 0.6 m.

In contrast to the relative homogeneity of the system of seagrass beds, the impounded marshes of Merritt Island and the barrier island east of Mosquito Lagoon do not have a uniform flora either in species composition or species density (Snelson 1976). This is due partially to variations in salinity and water level resulting from differing degrees of isolation among the impoundments. In the impoundment at the southern end of the Mosquito Lagoon studied here (I1) the marsh was broken by large expanses of water bordered by stands of black mangrove (Avicennia germinans); however, some white mangrove (Laguncularia racemosa) and button mangrove (Conocarpus erecta) were also present. The open waters were found to have seasonal growths of Chara, which in some locations filled the water column.

The northern impoundment canal (I2) was located approximately 200 m from site S2. This canal, formed by draglinning, is nearly continuous around the periphery of Van's Island and is approximately 1.25 m deep with a width of 15 to 20 m. During the dry season, it is the only standing water in the area sampled; however, during the rainy season this canal is only a part of the large marsh surface covered by water. The dominant vegetation was low-fringing black mangroves with some button mangroves along the dike and occasional growth of Chara.

METHODS

Sampling was done once each month during the period July 1978 through August 1979 for sites I1, S1, and S2. Site I2 was sampled monthly from August 1978 through August 1979. Each sampling effort consisted of measuring air and water temperature, salinity, depth, and submerged macrophyte density and collecting samples of macrozooplankton, fish, and larger epibenthic invertebrates. Benthic infauna were collected quarterly at each site in October 1978 and January, April, and July 1979. Site I1 was also sampled in May 1979.

Physical Data

Physical data collected at each site included measurements of air temperature in the shade, water temperature, salinity, and water depth in the areas sampled for fish. Maximum-minimum thermometers were submerged at sites I1, I2, and S2, and readings were taken each month and the thermometers reset. Salinity samples were taken at mid-water depth and analyzed using a temperature-correcting optical refractometer. In November 1979, surface sediment samples were taken at I1 and S2 and the percentage of combustible material determined by ignition in a 475°C oven for 8 hours.

Rainfall and average monthly air temperatures are from recordings taken at Patrick Air Force Base 60 km south of Mosquito Lagoon.

Zooplankton

Each month, three replicate 10-m length tows were taken at each site using a 363 μ mesh net with a diameter of 0.3 m and length of 1 m. The contents of each tow were individually preserved in 5% buffered formalin. Beginning in October ctenophores were counted prior to preservation. Ctenophores in earlier samples broke down rapidly and are, therefore, underestimated in data from July through September 1978.

Specimens were identified only at the most practicable taxonomic level during sorting and counting. Prior to sorting samples with a large amount of flocculent material, a small amount of dissolved rose bengal was added to stain the plankton and improve sorting efficiency.

The mesh size and length of tows were expected to produce comparatively dilute plankton samples but were considered adequate for the purpose of making a qualitative comparision between the impoundments and seagrass beds.

Benthic Infauna

Sampling the benthic infauna was done at a random location adjacent to the areas seined for fish. Five adjacent cores were taken from this area using a PCV coring tube with an inner diameter of 10.5 cm driven to a depth of 10 cm of solid sediment. Each core sampled 86.6 cm^2 of bottom area. At site I1 this produced a sample of 7-10 cm of flocculent material on top of the 10 cm of consolidated sediments. Sites I2, S1, and S2 did not have deep layers of unconsolidated material.

The contents of each core were sieved in the field to retain materials larger than 500 microns. The retained material was

preserved in 10% buffered formalin. After sorting and identification of core contents, representative subsamples were taken to determine dry weights and, for some gastropods and bivalves, ash-free dry weights per individual.

Standing crops of dry weights were converted to standing crop energy units by using published energy content values (Cummins and Wuycheck 1971, Thayer et al. 1973, Whitfield 1980).

Primary Production Processes

The above-ground standing crop of macrophytes from five randomly thrown 0.25 m^2 quadrats was harvested each month. Samples were taken in waters 50-75 m from shore at sites S1 and S2, along the edge of the canal at I2, and 25-50 m from shore at I1. The harvest from each toss was returned to the lab, where shell and detrital materials were rinsed off prior to drying to constant weight at 80°C.

The yearly net primary production of seagrass at sites S1 and S2 was calculated as two times the maximum standing crop (McRoy and McMillan 1977), assuming 1 mg dry weight is equivalent to 16 joules. The contribution of epiphytes to seagrass community net production was not evaluated; present work by the Harbor Branch Consortium (R. A. Gibson, personal communication) may shed some light on the contribution of epiphytes to net production within the seagrass beds of the Indian River.

Net primary production for site I1 was computed in two components: the contribution of the green algae Chara and the litter fall from the mangroves, primarily blacks (Avicennia). Production for Chara was calculated at 1.5 times the maximum standing crop (Rich et al. 1971);

mangrove litter production was calculated after determining a leaf area for the mangroves during the summer of 1979. Leaf area was calculated using the modified plumb-bob technique used by Benedict (1976). The technique was applied at five random sites, with ten replicates at each site. Production was then calculated using a ratio of leaf area index to litter production for Florida mangrove forests derived from Pool et al. (1974). Based on forest descriptions in Pool et al. (1974) leaf turnovers per year were assumed to be 1.0 and the ratio of leaf litter to wood litter to be 3:1. Dead leaves prior to falling were assumed to contain 20.17 J/mg (Heald 1969) and twigs 17.86 J/mg (Golley 1961) on a dry weight basis.

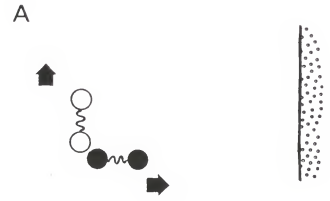
The percentage of marsh covered by open water versus mangrove canopy was determined by planimetry (cut and weigh) of recent aerial photographs of the I1 sampling area. This provided a proration to use in computing total marsh production from Chara and mangrove production data.

At site I2, the impoundment canal, the input of detritus was considered to be a complex interaction, varying with the season, of variable water transports to and from the impoundment flats. Therefore, an estimate of net primary production available within the canal habitats would be premature, based only on limited Chara and fringing mangrove production data.

Fishes

Shrimp, crabs, and fish were quantitatively sampled each month at sites I1, S1, and S2 by open-water seining as shown in Figure 2. Each net was 10 m in length, with a bar mesh of 3.18 mm. The sampling team

Figure 2. Diagrammatic aerial view of the open water sweep seine techniques; see text for explanation. Open circles = sweep net, closed circles = barrier net.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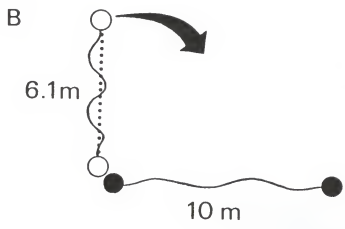
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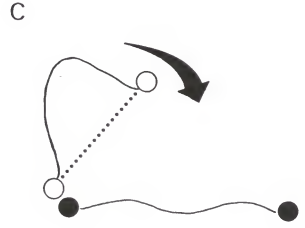
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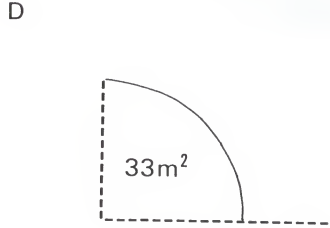
D
33m²

proceeded as a tight group to the edge of the area to be sampled, and immediately deployed the two nets, a sweep and a barrier, at right angles to each other. The barrier net was set perpendicular to the beach area and the sweep net, set on the deep water end of the barrier, was swept toward the shallows. The 10-m sweep net was tethered at a fixed distance of 6.1 m, sampling a bottom area of 33 m^2. The two nets were pursed and removed from the water for sorting. Site I2, the impoundment canal, was sampled using a beach seine. The sweep net was run out 6.1 m from the shoreline and perpendicular to it. The net was then swept to the beach. This covered 33 m^2 of area, as in the open-water seining. Because the canal was approximately 1.1 m deep at the end of the 6.1 m sweep net, the volumes of water swept in the two techniques were comparable. Three replicate quantitative samples were taken at each site.

Early attempts using a portable drop net (Adams 1976a) that sampled an area of 9 m^2 were found to be very labor-intensive and did not significantly alter the density, species number, or size classes found using open water seining. Gilmore et al. (1976) discussed the effect of sampling with drop nets for Indian River seagrass systems. He pointed out that due to the size of open sand and grass patches, drop samples can be strongly biased, while larger samples from seining cover a greater diversity of open sand and seagrass areas may be less biased. However, extremely large seines can underestimate several groups such as the gobies and pipefishes. The techniques used here are an attempt to compromise between drop-net and large sweep-net techniques.

Fish and invertebrate species collected were bagged in plastic and stored on ice. Samples were returned to the lab for processing as

soon as possible. Fish and invertebrates were sorted and identified; the fish were partitioned into standard length-size ranges of 5 mm, i.e. 0-5 mm, 6-10 mm, etc; crabs were measured across the width of the carapace. After drying for 48 hrs in a forced air oven at 80°C, dry weights were recorded for each size class group for each species of fish, for the total of each shrimp sample, and for each crab individually.

A qualitative seine sweep was taken each month at sites S1 and S2 with a 20 m bag seine, also of 3.18 mm bar mesh. An area of 1000-2000 m^2 was swept at each site. Fish and invertebrates collected were sorted and any species not found in the quantitative seine were preserved in 25% buffered formalin. The remaining catch was subsampled to augment the various size class categories of species collected in the quantitative seines to provide an adequate sample size, in terms of mass, for calorimetry. The samples were separately bagged and also stored on ice for immediate processing and drying on returning from the field.

Calorimetric Processing

After recording dry weights of individual size classes for each fish species, the various size classes of the dominant species were grouped into age classes (Table 1) according to the technique of Adams (1976a). These samples were then processed according to the general procedures outlined by Cummins and Wuycheck (1971); however, no carbonate fractions were determined. For determination of ash-free dry weights, subsamples were burned at 475°C for four hours to avoid burning off carbonates (Paine 1971). Calorimetry was done using an

Table 1. Age class groupings of common seagrass and impoundment of fishes in mm of standard length.

Species	Age Class			
	Pre-juv	Juvenile	Adult	Rep Adult
Anchoa mitchilli		≤50	>50	
Archosargus probatocephalus		25-50	>50	
Bairdiella chrysoura		10-85	>85	>130
Cynoscion nebulosus		25-200	>200	
Cyprinodon variegatus	10-14	15-24	25-35	>35
Eucinostomus sp.		15-55	>55	
Fundulus grandis		15-30	>30	
Gambusia affinis		≤20	>20	
Gobiosoma robustum		9-15	>15	
Lagodon rhomboides	15-50	51-85	>85	
Leiostomus xanthurus		17-85	>85	
Lucania parva		8-25	>25	
Lutjanus griseus		10-175	>175	
Menidia sp.		20-60	>60	
Microgobius gulosus		≤30	>30	
Paralichthys albigutta		≤95	>95	
Poecilia latipinna		≤20	>20	
Strongylura notata		45-200	>200	
Syngnathus scovelli		≤60	>60	
Trinectes maculatus		18-45	>45	

automatic adiabatic calorimeter equipped with a digital thermometer, printer, and programmer (Parr Instrument Company, Moline, Illinois). Operating procedures followed the Parr procedures manual directly (Parr 1969). Two 1 g replicate samples were taken for percent water and ash content determination at the same time the three replicate 1 g pellets were pressed prior to bombing. Over 90% of the materials tested gave a coefficient of variation ("C.V.") of less than 1%, using three replicates. The C.V. was less than 3% for 99% of the samples. Golley (1961) and Paine (1971) recognize a coefficient of less than 3% as a satisfactory variation for biological materials. Results are expressed as joules per milligram of ash free dry weight.

Production

As defined by Ivlev (1966), production is the total amount of fish tissue produced during any given time interval, including that of individuals that did not survive to the end of that interval. Monthly production is then calculated as the product of the growth per individual and fish numerical density.

Production for each species was calculated after Ricker (1946) and Allen (1950) as

$$P = G\bar{B}$$

where

$$G = \frac{\ln \bar{w}_2 - \ln \bar{w}_1}{\Delta t}$$ is the coefficient of instantaneous growth,

$$\bar{B} = \frac{B_1(e^{G-Z} - 1)}{(G-Z)}$$ is the average biomass, and

$$Z = \frac{-(\ln N_1 - \ln N_2)}{\Delta t}$$ is the instantaneous coefficient of population change attributable to mortality and migration,

and W_1 and W_2 are the mean weights at time t_1 and t_2, respectively, and N_1 and N_2 are the numbers of fishes present at times t_1 and t_2, respectively.

Day et al. (1973), Adams (1976b), and Chapman (1978) discussed some of the important assumptions of the applications of this model. As Adams (1976b) pointed out, estuarine and seagrass fishes usually show marked immigration and emigration which affect estimates of N. This is probably more significant at sites S1 and S2 than at I1 and I2. However, Chapman (1978) pointed out that there is no need to correct production data for the immigration and emigration of fishes, provided fish density and size-class specific growth are estimated often enough to assess abundance and growth during the sampling period. Day et al. (1973) used three-week sampling intervals, while Adams (1976a) used four-week intervals as done in this study.

Respiration

The resting energy of metabolism was estimated from Winberg's (1956) equation, $Q = 0.321\ W^{0.79}$, as a general equation for marine fish at 20°C. Metabolism for each species was calculated at an average weight per individual at the median water temperature during the sampling period by applying Krogh's (1916) temperature correction factors. This rate of oxygen use per hour by one average-weight individual weighing X g dry weight was converted to a population total of joules burned per month at each site using a conversion factor of 14.07 J/mg of oxygen (Mann 1978).

The energy cost specific to utilization of food, apparent specific dynamic action, and the metabolic cost of foraging for food were both found to be significant portions of the energy budgets of fish populations studied by Kerr (1971a,b,c). Reviews by Webb (1978) and Mann (1978) discuss the relationship between resting metabolism and true energy costs in nature. According to Mann (1978), Winberg II, a doubling of the equation above (Winberg I), appears to be a useful approximation of the metabolism of a fish which optimizes its growth rate in nature (Edwards 1968, Ware 1975). Winberg II is used here as the estimate of respiration within the fish community.

Consumption and Energy Budgets

Annual energy consumption per species in both habitat types was calculated as a percentage of the sum of respiration plus production. Winberg (1956) found assimilation efficiencies for freshwater fishes between 76% and 96.6%. The average values assumed were 85% of calories of the diet were assimilated and 15% lost as feces. He also argued that, with a range of 3-7% of the energy lost as urine added to fecal loss, a total of 20% of ingested energy was lost through egestion and excretion.

Winberg's equation as applied here is

$$C = 1.25\ (P + R)$$

where

C = annual consumption of energy,

R = annual metabolic energy loss,

P = annual production energy.

Community annual consumption is then compared between the various sites. Interspecific comparisons of consumption should be done cautiously, due to the broad range of assimilation efficiencies found for different fish species in nature (Webb 1978).

Fish community energy budgets for each site were then constructed by the addition of each species' totals for consumption, production, and respiration during the year. Ecological efficiencies were then calculated for each community and used to compare communities.

RESULTS

Diagrams summarizing the major environmental influences, primary production sources, and energy flows for the impounded marshes and seagrass beds are presented in Figure 3. These diagrams depict the conceptual framework for presentation of the results of this study and the subsequent discussion of each community.

Physical Environment

The average values and the ranges of temperature and salinity for the four sites show an interesting pattern (Tables 2 and 3). The yearly range of temperatures (Table 2) found in the two impoundment habitats, I1 and I2, and one seagrass bed, S2, were nearly identical; however, the average range per month of temperatures experienced at I2 was significantly smaller (Student's t, $p < 0.05$) than those ranges for I1 and S2. This reduced environmental flux at I2 is assumed to result from the deeper water buffering rapid daily temperature fluctuations. Site I2 had narrower average monthly temperature ranges than site S2, but not significantly so. Overall, water temperatures closely paralleled the average air temperatures and the two were roughly equal during January, February, and March.

Significant differences were found in the average salinities at the four sites. Site I1 was significantly lower than the other three sites (Student's t, $p < 0.01$). Site I2 was significantly higher than

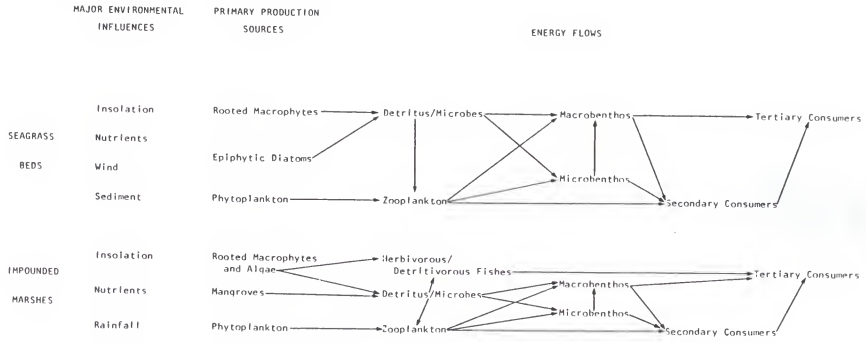

Figure 3. Summary diagrams of generalized seagrass bed and impounded marsh energy flows into the fish community.

Table 2. Median water temperatures and average monthly air temperatures during the sampling period; absolute minimum, absolute maximum and temperature ranges from submerged maximum/minimum mercury thermometers.

Year & Month	Water Temp(°C)			Air Temp(°C)
	I1	I2	S2	Cape Canaveral
1978 August	----	----	31.5	25.6
September	31.0	31.0	31.0	25.0
October	26.0	30.0	24.0	22.0
November	23.0	23.0	22.5	22.0
December	21.5	22.5	20.4	17.0
1979 January	15.0	15.0	----	15.0
Februrary	16.4	16.8	17.5	15.0
March	18.5	19.3	18.5	18.0
April	24.0	25.5	24.5	22.8
May	27.5	27.0	----	23.9
June	29.0	31.5	29.0	26.7
July	20.5	33.0	----	28.3
August	31.0	31.3	----	27.2
Absolute minimum	6.0	8.0	8.0	
Absolute maximum	39.0	37.5	39.0	
Maximum monthly range width	17.5	15.5	19.0	
Average monthly range width	14.7	10.8	15.3	

Table 3. Salinity at each site monthly and total rainfall at Cape Canaveral.

Year & Month	Salinity (°/oo)				Rainfall (mm)
	I1	I2	S1	S2	Cape Canaveral
1978 August	14	38	35	38	32
September	16	38	32	36	88
October	17	36	38	36	56
November	20	36	34	34	16
December	28	38	38	38	103
1979 January	10	28	18	25	178
Februrary	12	32	20	33	32
March	13	32	22	34	39
April	18	34	----	38	19
May	15	32	24	30	142
June	20	35	32	35	116
July	18	34	35	34	85
August	16	36	36	37	228
Average	16	34	30	34	
Range	10-28	28-38	18-38	25-38	

S1 (Student's t, $p < 0.01$), while S1 and S2 were not significantly different from each other.

As was the case with temperature, the stabilizing influence of greater water depth on yearly fluctuations is seen in the narrower range of salinity found at site I2, as compared to the other three sites. In comparing S1 and S2, the greater range of salinity at S1 is believed to be due to the isolation of the shallow portion of the lagoon where site S1 is located (Eddy Creek). This possibly reduces mixing and, consequently, the waters of S1 are diluted relatively more during periods of heavy rainfall. The most remarkable change in salinities was a drop of 20°/$_{oo}$, which occurred at S1 from December to January due to the heavy rains the area received in late December and early January.

The seasonality of rainfall in the Mosquito Lagoon area would appear to modify the rain's influence on depressing salinity in the system. Two peak periods of rainfall were observed, winter and early summer. During the winter, when rates of evaporation were relatively low, salinity was markedly depressed by heavy rainfall and did not recover rapidly. However, during the summer, a period of rapid evaporation, heavy rains did not depress salinities to the same degree as winter rains, nor for as long a time. Therefore, the seasonality of rainfall, as well as amount, markedly affected both the level and fluctuations of salinity within the shallow water systems studied.

The percentage of combustible organic material in the surface sediment at I1 was over five times greater than that found at S1 (22.6% vs. 3.9%). With sample sizes of 9 and 8, respectively, this difference is highly significant (Student's t, $p < 0.001$). Therefore, the yearly

accumulation of detrital material is assumed to be much greater within the impoundments than in the shallow seagrass bed. However, some of the detritus originating in the shallows may possibly be transported from the seagrass beds and deposited in deeper waters of the lagoon. Thomas (1974) found amounts of organic carbon in the sediments of barrow pits and infrequently dredged portions of the intracoastal waterway to be 2 to 3 times higher than the shallower seagrass beds. However, the percentage of net detrital production exported to deeper water storage in the open lagoon is not known.

Primary Production

Estimates of net primary production for three sites are presented in Tables 4 and 5. The ratio of mangrove production to Chara production within the impoundments was approximately 4:1. The ability to extrapolate from the estimates for I1 to the entire impounded marsh has not been demonstrated. Analysis of infrared aerial photographs to determine plant surface areas within the impoundments is now being attempted using facilities of the Kennedy Space Center. However, the spectral sensitivity of films presently available does not appear to be great enough and will delay estimates until a great deal of ground-truth work is done.

Zooplankton

The twelve months of zooplankton collections were divided into four seasonal quarters (Table 6) based on rainfall and air temperature patterns (Tables 2 and 3). By taking the average of the collections for each of the three month periods, some of the temporal

Table 4. Net primary production ($kJ \cdot m^{-2} \cdot y^{-1}$) entering the aquatic system at site I1: units given for each value, numbers in parentheses are one standard error, N--sample size.

Site I1	
Mangrove	
Leaf area index	1.66 (0.47), N = 50
Leaf weight/leaf area (g/m^2)	180 (51), N = 10
Net production as litter into the aquatic system ($kJ \cdot m^{-2} \cdot y^{-1}$)	7463
Percentage of marsh covered by mangroves	46%
Net Production ($kJ \cdot m^{-2} \cdot y^{-1}$)	3433
Chara	
Maximum standing crop (g/m^2)	63.98 (51.66), N = 5
Minimum standing crop (g/m^2)	0.0, N = 5
Net production in open water ($kJ \cdot m^{-2} \cdot y^{-1}$)	1648 (1331)
Percentage of open water	53%
Net Production ($kJ \cdot m^{-2} \cdot y^{-1}$)	873 (705)
Total marsh net production ($kJ \cdot m^{-2} \cdot y^{-1}$)	4306

Table 5. Net primary production and standing crops of seagrasses at sites S1 and S2; numbers in parentheses are one standard error, N--sample size.

	S1	S2
Maximum standing crop (g/m^2)	75.83 (24.37), N = 5	116.5 (20.14) N = 5
Minimum standing crop (g/m^2)	12.11 (4.4), N = 5	8.74 (6.34), N = 5
Net Production ($kJ \cdot m^{-2} \cdot y^{-1}$)	2413 (387)	3707 (320)

Table 6a. Mean standing crop of zooplankton (Number/m^3), September to November 1978 at each sampling site.

Taxa	I1	I2	S1	S2
Cnidarians	---	1.6	0.2	1.0
Nematodes	21.0	0.8	0.5	2.8
Polychaetes	0.3	0.6	0.8	0.3
Gastropods	2.0	0.2	---	---
Bivalves	0.2	---	---	0.6
Ostracods	12.0	0.2	0.2	2.7
Copepod larvae	---	---	0.7	---
Calanoid copepods	1.0	1.0	1.7	5.6
Cyclopoid copepods	---	---	0.2	0.3
Harpacticoid copepods	---	0.2	1.0	1.0
Cypris larvae	---	---	0.2	---
Mysids	---	---	0.2	---
Amphipods	0.5	---	---	---
Caridean shrimp	1.2	0.4	2.0	15.1
Brachyuran larvae	0.2	0.2	1.0	1.0
Larvaceans	---	---	3.3	---
Chaetognaths	---	0.2	0.2	2.1
Other taxa	1.6	---	0.8	0.7
Total	40.0	5.1	12.3	33.2

Table 6b. Mean standing crop of zooplankton (Number/m^3), December 1978 to February 1979 at each sampling site.

Taxa	I1	I2	S1	S2
Cnidarians	---	---	---	0.6
Ctenophores	---	---	0.1	1.9
Nematodes	183.0	6.1	25.5	13.0
Polychaetes	0.2	2.7	1.0	1.0
Gastropods	1.4	---	---	---
Bivalves	---	---	1.1	0.7
Ostracods	1.6	0.2	8.8	3.5
Calanoid copepods	4.6	85.0	8.8	9.1
Cyclopoid copepods	1.2	0.3	2.1	0.4
Harpacticoid copepods	2.4	1.9	1.7	1.0
Cypris larvae	---	---	---	0.1
Mysids	---	---	0.7	---
Cumaceans	---	0.2	0.3	0.3
Isopods	0.2	0.2	3.9	5.7
Amphipods	---	2.4	3.9	1.1
Caridean shrimp	0.4	1.1	73.4	33.9
Brachyuran larvae	---	---	0.5	0.1
Pycnogonids	---	---	0.1	0.1
Hemipteran exoskeleton	0.4	4.0	---	0.7
Mosquito larvae	---	2.2	---	---
Chaetognaths	---	---	0.7	1.0
Fish eggs	---	1.3	0.1	---
Fish larvae	---	0.8	1.0	0.3
Other taxa	3.0	0.1	0.1	0.4
Total	197.9	107.6	134.0	74.0

Table 6c. Mean standing crop of zooplankton (Number/m^3), March to May 1979 at each sampling site.

Taxa	I1	I2	S1	S2
Cnidarians	1.1	2.8	---	0.6
Ctenophores	---	---	0.01	15.7
Nematodes	282.3	15.7	17.6	34.0
Polychaetes	1.4	1.4	0.6	1.1
Gastropods	0.3	0.6	0.2	5.7
Bivalves	---	0.2	1.1	0.8
Ostracods	1.1	0.8	4.6	1.9
Copepod larvae	1.0	---	---	---
Calanoid copepods	37.1	152.8	56.4	2.7
Cyclopoid copepods	5.0	0.3	---	---
Harpacticoid copepods	6.4	1.7	0.9	3.5
Isopods	---	0.3	0.5	1.4
Amphipods	0.6	0.6	0.6	1.1
Caridean shrimp	3.0	3.3	51.9	25.8
Brachyuran larvae	0.3	1.9	43.7	2.4
Chaetognaths	---	---	3.9	0.2
Fish eggs	---	---	0.2	---
Fish larvae	---	0.2	1.7	0.6
Other taxa	0.3	1.9	0.2	0.8
Total	339.9	184.5	184.4	98.3

Table 6d. Mean standing crop of zooplankton (Number/m^3), June to August 1979 at each sampling site.

Taxa	I1	I2	S1	S2
Cnidarians	---	---	0.3	2.7
Ctenophores	---	---	9.1	0.2
Nematodes	48.4	4.7	21.2	27.8
Polychaetes	---	---	0.9	2.0
Gastropods	---	---	1.4	1.7
Ostracods	1.3	---	4.6	3.0
Copepod larvae	0.8	---	0.2	0.2
Calanoid copepods	127.8	8.6	16.5	133.6
Cyclopoid copepods	1.1	---	0.8	0.5
Harpacticoid copepods	2.4	0.5	4.1	9.9
Isopods	---	---	1.6	7.5
Amphipods	0.2	0.3	---	1.3
Caridean shrimp	3.5	0.2	14.8	64.6
Brachyuran larvae	3.3	4.7	69.3	4.1
Hemipteran exoskeletons	---	1.1	---	---
Chaetognaths	---	---	0.5	3.8
Fish eggs	---	---	12.3	---
Fish larvae	---	---	1.1	0.9
Other taxa	0.03	0.4	1.1	1.8
Total	188.7	20.5	159.8	265.3

variations in standing crops of zooplankton is lost, making the sites, in some cases, appear more similar. However, the zooplankton here are being used to interpret broad aquatic community differences in the four sites studied, and this loss of information is not considered critical.

The most abundant groups found in the water column were nematodes, calanoid copepods, and caridean shrimp. Several other groups that were not as abundant but showed noticeable site and/or seasonal differences in distribution were ostracods, brachyuran larvae, and chaetognaths. Several groups such as the nematodes and harpacticoid copepods are not normally considered zooplankton, but are so considered here because, due to shallowness and windmixing, they are constantly in the water column. The exclusion of such forms would not seem appropriate when trying to reflect on the biological activity of the water column and, ultimately, how such differences might relate to fish-community structure and function.

The water column at site I1 was dominated by nematodes, except in midsummer when large swarms of calanoid copepods appeared. At this same time caridean shrimp and brachyuran larvae were reaching their peak abundances at site S1.

Site I2 was characterized by the sharp seasonality of calanoid copepods. During the spring, densities peaked, only to crash dramatically by midsummer. Midsummer in general was a period of very low plankton standing crop at I2 relative to the other sites.

The seagrass sites were distinguished somewhat from the impoundment sites by the greater densities of caridean shrimp and brachyuran larvae and were distinguished between themselves on the seasonality

of these same taxa. Caridean shrimp densities reached a peak at S1 during the winter and spring, whereas they peaked at S2 in midsummer. Brachyuran larvae were much denser at S1 than any other site, and reached a peak density during midsummer as they also did at S2. Sites S1 and S2 were also distinguished by consistent chaetognath populations.

Overall, the spring was the period of peak zooplankton densities for both impoundments, while one seagrass bed peaked in spring and the other in midsummer.

Macrobenthos

The results of the quarterly sampling at each site are shown in Tables 7, 8, 9, and 10. The values shown in Table 11 were used to convert dry weight to joules. Nematode densities were converted to biomass using 1.46 µg/nematode (Day et al. 1973) and copepod densities were converted using 18 µg/copepod, a general value cited by Day et al. (1973). Based on average annual standing crops of energy, sites I1 and S2 were significantly lower than sites I2 and S1 (Student's t, $p < 0.01$). This is also reflected in the number of major storages, here defined as taxa with average standing crops in excess of 2 kJ/m^2, at each site. Diversity of storages is assumed to be indicative of the diversity of energetic pathways within the system. Sites I1, S2, I2, and S1 had 3, 6, 7, and 10 such major energy storages, respectively.

The contributions of major taxa to the annual average standing crop are shown in Table 12. Both impoundment sites were dominated by bivalves, whereas the seagrass sites had a much larger storage in polychaetes and, in general, had greater equitability between storage compartments. Major storages unique to the two site types were

Table 7. Site II's average quarterly and average annual densities (Number/m^2) and standing crops of energy (kJ/m^2) for the major groups of benthic invertebrates.

Taxa	October		January		April		July		Average	
	Density	Energy	Density	Energy	Density	Energy	Density	Energy	Density	Energy
Polychaeta	23	0.16	462	2.41			254	1.15	185	0.93
Oligochaeta			23	0.08			277	1.00	75	0.54
Amphipoda	69	0.48	162	2.51					58	0.75
Decapoda			69	6.04	23	2.01			23	2.01
Isopoda	92	2.30	416	4.13	139	1.38			162	1.95
Copepoda					23	<0.01			6	<0.01
Cumacea					92	4.33			23	1.00
Ostracoda	254	<0.01	93	<0.01			393	<0.01	185	<0.01
Gastropoda	23	88.33	69	60.56					23	37.22
Bivalvia	611	35.56	382	16.47	3996	154.80	83	25.91	1268	58.18
Nematoda	23	<0.01							6	<0.01
Sipuncula					23	0.39			6	0.10
Totals	1095	126.83	1676	92.21	4296	162.91	1007	28.06	Annual 2020	Average 102.77

Table 8. Site I2's average quarterly and average annual densities (Number/m^2) and standing crops of energy (kJ/m^2) for the major groups of benthic invertebrates.

Taxa	October		January		May		July		Average	
	Density	Energy	Density	Energy	Density	Energy	Density	Energy	Density	Energy
Polychaeta	5278	14.39	7969	32.59	3626	14.83	1524	4.85	4599	16.67
Oligochaeta	8892	4.78	3626	6.53	20857	37.58	670	3.74	8511	13.17
Amphipoda	38803	46.95	7858	24.36	3788	9.40	2194	3.06	13161	20.95
Decapoda			439	6.58					110	1.65
Tanaidacea	1351	0.51	3303	6.27	762	1.89	439	1.86	1464	2.64
Isopoda			323	1.09	439	7.06	1663	3.16	606	2.83
Copepoda			69	<0.01	1432	0.37	162	<0.01	416	0.10
Cumacea					23	1.08			6	0.27
Ostracoda	32	<0.01							8	<0.01
Gastropoda			69	15.55	46	10.37			29	6.48
Bivalvia	3168	381.36	1176	242.92	1277	230.53	4378	166.89	2500	255.00
Platyhelminthes	16	0.43	139	3.67	92	2.45			62	1.64
Nematoda	773	0.20	254	<0.01	3095	0.08	10648	0.28	3693	0.14
Nemertinea					346	7.64			87	1.91
Sipuncula							23	0.29	6	0.07
Totals	58313	448.65	25225	339.58	35783	315.65	21701	184.14	Annual 35257	Average 323.50

Table 9. Site S1's average quarterly and average annual densities (Number/m^2) and standing crops of energy (kJ/m^2) for the major groups of benthic invertebrates.

Taxa	October		January		April		July		Average	
	Density	Energy	Density	Energy	Density	Energy	Density	Energy	Density	Energy
Polychaeta	1617	128.58	6629	138.57	5636	345.74	4735	31.20	4654	161.00
Oligochaeta	23	<0.01	2125	0.77	323	5.83	139	0.03	653	1.66
Amphipoda			2240	7.99	323	6.02	231	0.14	699	3.54
Decapoda			231	8.46	254	0.09	69	2.17	139	2.68
Tanaidacea			23	0.08	69	0.23	323	1.09	98	0.35
Isopoda			2287	11.70	23	1.18	577	2.53	722	3.85
Copepoda	23	<0.01			23	<0.01	23	<0.01	17	<0.01
Cumacea			693	7.90	92	4.33			196	8.06
Ostracoda	93	0.02			46	<0.01	947	0.28	272	0.08
Ophiuroidea			670	235.53	46	16.11	69	20.60	196	63.06
Gastropoda	69	264.95	254	222.07			1732	59.81	514	136.71
Bivalvia	2480	66.05	1340	25.85	785	79.86	1732	50.33	1584	55.52
Platyhelminthes			46	0.20					12	0.05
Nemertinea	46	5.28	92	2.41	46	1.11	46	1.11	58	2.48
Nematoda	69	<0.01	370	<0.01	624	0.02	393	0.01	364	0.01
Sipuncula			208	7.97			23	0.03	58	2.00
Totals	4397	464.91	17208	669.51	8290	460.54	11039	164.34	Annual 10286	Average 441.06

Table 10. Site S2's average quarterly and average annual densities (Number/m^2) and standing crops of energy (kJ/m^2) for the major groups of benthic invertebrates.

Taxa	October		January		April		July		Average	
	Density	Energy	Density	Energy	Density	Energy	Density	Energy	Density	Energy
Polychaeta	1963	38.36	5451	99.10	4158	132.25	7299	99.50	4718	92.31
Oligochaeta	347	0.50	1363	1.96	601	2.16	739	9.86	763	3.62
Amphipoda	162	0.30	2726	2.54	208	0.10	323	0.50	855	0.86
Decapoda	23	0.52	46	1.05	23	0.52	69	1.57	40	0.42
Tanaidacea	46	0.16	46	0.16	46	0.16	139	0.47	64	0.24
Isopoda			116	1.35	23	0.27	162	0.47	75	0.52
Copepoda	1155	0.30	416	0.11	69	<0.01	139	0.03	445	0.11
Cumacea	23	0.26	46	0.53	92	4.33			40	1.28
Mysidacea	23	0.30							6	0.08
Ostracoda	46	0.45	70	0.60					29	0.26
Hydroida							162	0.14	41	0.04
Ophiuroidea			23	5.56	46	11.17	92	22.23	40	9.74
Gastropoda	23	5.18			23	5.18	162	36.29	52	11.66
Bivalvia	3095	29.98	20626	34.96	2541	12.30	416	35.28	6670	28.12
Platyhelminthes							93	0.41	23	0.10
Nemertinea	139	3.89	46	1.30	23	0.51			52	1.43
Nematoda	601	0.02	139	<0.01	416	0.01	439	0.01	394	0.01
Sipuncula	92	0.26	46	5.83	393	4.85	23	0.98	139	2.98
Totals	7738	80.48	31163	155.06	8662	173.82	10258	207.69	Annual 14456	Average 154.28

Table 11. The values and authorities cited used to covert standing crops on a dry weight basis to standing crops on an energy basis, for the benthic invertebrate groups common in the impoundments and seagrass beds.

Taxa	Conversion Factor (J/mg dry wt)	Reference	Notes
Polychaeta	22.72	3	
Oligochaeta	18.02	5	
Amphipoda	15.51	3	
Decapoda	17.43	3	
Tanaidacea	14.62	5	Isopod value
Isopoda	14.62	5	
Gastropoda	17.81	3	
Bivalvia	20.06	1	
Platyhelminthes	22.05	1	
Sipuncula	14.19	1	
Cumacea	15.62	4	
Nemertinea	20.04	1	average of Oligochaeta and Platyhelminthes
Ophiuroidea	5.71	3	
Hydroidea	12.08	1	
Nematoda	18.01	2	
Ostracoda	15.62	4	Cumacea value
Mysidacea	15.62	4	Cumacea value
Copepoda	14.49	4	

1 - Cummins and Wuycheck (1971)
2 - Day et al. (1973)
3 - Thayer et al. (1973)
4 - Blaber (1979)
5 - Whitfield (1980)

Table 12. Percentage of the average annual standing crop of energy for major benthic invertebrate groups at each site.

Taxa	I1	I2	S1	S2
Polychaeta	--	5	37	60
Oligochaeta	--	4	--	2
Amphipoda	--	6	--	--
Decapoda	2	--	--	--
Ophiuroidea	--	--	15	6
Gastropoda	36	2	31	8
Bivalvia	57	79	13	18
Sipuncula	--	--	--	2

decapods and amphipods in the impoundments and brittle stars and sipunculids in the seagrass beds. Two subgroups, I1-S2 and I2-S1, which departed from the original habitat groups I1-I2 and S1-S2, appeared based on average annual standing crop and on standing crop of molluscs. Site I1 had a higher percentage of bivalves than I2, but a lower percentage of gastropods. The same was true for S2 as compared to S1. Sites I2 and S1 are, therefore, distinctive from their comparison sites I1 and S2, respectively, for two reasons. First, they have higher standing crops and secondly they have a higher bivalve to gastropod ratio than their comparison sites.

Comparing the four sites seasonally, the most distinctive feature is that each site appears to operate on a different schedule of maximum and minimum standing crops of energy. Site I1 is bimodal with peaks in fall and spring, I2 peaks in fall, S1 in winter, and S2 in the summer. Thus, the impoundments reached their peak standing crops in the fall and spring, while the seagrass beds peaked in winter and summer.

The magnitude of energy storage compartments and total standing crop, of course, are only structural comparisons of the macrobenthos, and do not reflect functional characteristics of the bottom communities. Therefore, significant structural differences found between sites and habitat types do not necessarily reflect differences in the rate of energy transfers within the benthic community.

Epibenthic Invertebrates

The dominant epibenthic invertebrates were caridean shrimp, primarily *Hippolyte pleuracanthus*, *Palaemonetes intermedius*, and

Table 13. Average annual density (Number/m^2) and standing crop of energy (J/m^2) of common large decapods at each site.

Taxa	I1		I2		S1		S2	
	Density	Energy	Density	Energy	Density	Energy	Density	Energy
Caridean shrimp	1.70	1106	8.34	6798	6.99	862	4.06	879
Penaeus sp.	<0.01	28	<0.01	65	0.02	631	0.37	2542
Callinectes sapidus					0.01	1230	0.02	861

Periclimenes americanus; penaeid shrimp, Penaeus duorarum and Penaeus aztecus; and the blue crab, Callinectes sapidus. Based on Odum (1971), these three groups represent a broad trophic spectrum and therefore should be functionally grouped together for very broad general comparisons, as done here to highlight the fate of net primary production in each system and to compare habitats and community structure. Several other species were collected, but in very low numbers (i.e. the mud crab, Neopanope packardii; the spider crab, Libinia dubia; the hermit crab, Pagurus bonairensis; and the snapping shrimp, Alpheus heterochaelis).

At each site, caridean shrimp were the numerically dominant group (Table 13). However, based on average energy content, blue crab and penaeid shrimp were dominant at sites S1 and S2, respectively. In comparing the yearly totals for each site, I1 had distinctively lower standing crops of the major epibenthic invertebrates than the other three sites. Site I2 was dominated by the influence of caridean shrimp, while S1 and S2 had more equitable distributions of standing crops among all three groups.

Fish Community Structure

Species Composition and Seasonality

A total of 44 fish species were found in the study (see Tables 14, 15, 16, and 17). Fourteen species were found in the impoundments, but none was restricted to these sites. Between the two impoundment sites, the difference in the species list is due to rare species. This is also the case when comparing the two seagrass beds; some relatively rare species were unique to one site or the other.

Table 14. Fish collected at site I1.

Species	1978						1979							
	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug
Cyprinodon variegatus	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Fundulus grandis												X	X	X
Lucania parva	X		X		X			X	X	X	X	X	X	X
Gambusia affinis		X	X	X	X	X		X		X	X	X	X	X
Poecilia latipinna		X	X							X	X	X	X	X
Menidia peninsulae	X	X	X	X	X	X	X		X	X	X	X	X	X
Menidia beryllina				X	X	X	X	X	X	X	X	X	X	X
Syngnathus scovelli									X	X				
Microgobius gulosus		X	X	X	X					X	X	X	X	X
Trinectes maculatus		X												
Totals	3	6	6	5	6	4	3	4	5	8	7	8	8	7

Table 15. Fish collected at site I2.

Species	1978						1979							
	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug
Anchoa mitchilli									X					
Cyprinodon variegatus		X	X	X	X		X	X	X	X	X	X	X	X
Floridichthys carpio						X	X							
Fundulus grandis		X	X	X				X	X	X	X	X	X	
Fundulus similis							X							
Lucania parva		X	X	X	X	X	X	X	X	X	X	X	X	X
Gambusia affinis		X	X	X	X	X	X	X	X	X	X	X	X	X
Poecilia latipinna		X	X	X	X	X	X	X	X	X	X	X	X	X
Menidia peninsulae		X	X	X	X		X	X	X	X	X	X	X	
Menidia beryllina				X	X		X	X	X			X	X	X
Syngnathus scovelli			X	X	X	X	X	X	X	X	X	X		
Mugil cephalus										X				
Gobiosoma robustum				X	X									
Microgobius gulosus		X	X	X	X	X	X	X	X	X	X	X	X	
Totals		7	8	10	9	6	10	9	10	9	8	9	8	5

Table 16. Fish collected at site S1.

Species	1978						1979							
	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug
Elops saurus									X					
Brevoortia sp.								X	X	X	X			
Anchoa mitchilli			X	X	X		X		X	X	X	X	X	X
Opsanus tau							X						X	X
Hyporhamphus unifasciatus									X					
Strongylura notata					X	X	X	X	X	X	X	X	X	X
Strongylura timucu										X				
Cyprinodon variegatus			X					X		X		X		
Floridichthys carpio			X			X		X	X	X	X	X	X	X
Fundulus grandis					X	X		X				X	X	X
Fundulus similis					X	X	X	X	X	X	X	X	X	X
Lucania parva	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Poecilia latipinna						X			X					
Menidia peninsulae	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Menidia beryllina								X						
Hippocampus zosterae			X					X	X					

Table 16. (Continued)

Species	1978						1979							
	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug
Syngnathus louisianae					X									
Syngnathus scovelli	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Oligoplites saurus						X								
Lutjanus griseus				X	X									
Diapterus auratus						X								
Eucinostomus sp.					X	X		X			X			X
Eucinostomus argenteus							X							X
Orthopristis chrysoptera												X		
Haemulon sciurus		X							X		X	X		X
Archosargus probatocephalus					X	X		X						
Lagodon rhomboides	X	X	X	X	X				X			X	X	X
Bairdiella chrysoura		X	X		X	X				X	X	X	X	X
Cynoscion nebulosus		X	X	X	X	X	X					X	X	X
Leiostomus xanthurus		X			X		X	X	X	X		X	X	
Mugil cephalus								X			X		X	X
Chasmodes saburrae			X											X
Gobiosoma robustum	X			X	X	X	X	X	X	X	X	X	X	X
Microgobius gulosus	X		X	X	X	X	X	X	X	X	X	X	X	X

Table 16. (Continued)

Species	1978						1979							
	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug
Paralichthys albigutta								X						
Paralichthys lethostigma									X					
Achirus lineatus								X		X		X		
Trinectes maculatus						X				X		X		
Totals	6	8	12	9	17	17	12	19	18	16	14	19	16	19

Table 17. Fish collected at site S2.

Species	1978						1979							
	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug
Brevoortia sp.									X					
Anchoa mitchilli		X		X				X	X	X				
Opsanus tau	X		X				X						X	X
Hyporhamphus unifasciatus									X	X				
Strongylura marina											X	X		
Strongylura notata	X	X			X					X			X	X
Strongylura timucu													X	
Cyprinodon variegatus						X	X	X				X	X	
Floridichthys carpio	X			X	X	X	X	X	X	X	X	X	X	X
Fundulus grandis				X		X	X				X	X	X	X
Fundulus similis							X				X			X
Lucania parva	X	X	X	X	X	X	X		X	X	X	X	X	X
Gambusia affinis			X											
Poecilia latipinna			X			X	X				X	X	X	X
Menidia peninsulae	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Menidia beryllina							X							

Table 17. (Continued)

Species	1978						1979							
	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug
Hippocampus erectus										X				
Hippocampus zosterae							X					X	X	X
Syngnathus louisianae											X		X	X
Syngnathus scovelli	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Oligoplites saurus	X									X				
Trachinotus falcatus				X										
Lutjanus griseus				X										
Lutjanus synagris													X	
Eucinostomus sp.			X	X		X	X			X		X		X
Eucinostomus argenteus				X	X									
Eucinostomus gula	X													
Haemulon sciurus	X			X					X	X	X	X		X
Archosargus probatocephalus		X		X	X	X	X							
Lagodon rhomboides	X	X		X	X	X			X	X	X	X	X	X
Bairdiella chrysoura		X	X	X				X				X	X	X
Cynoscion nebulosus		X	X	X	X					X			X	X
Leiostomus xanthurus	X			X	X			X	X	X	X		X	
Chaetodipterus faber	X													

Table 17. (Continued)

Species	1978						1979							
	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug
Mugil cephalus				X			X	X		X				
Gobiosoma robustum	X		X	X	X	X	X	X	X	X	X	X	X	X
Microgobius gulosus	X		X	X	X	X	X	X	X	X	X	X	X	X
Paralichthys albigutta					X	X			X		X			
Paralichthys lethostigma											X			
Achirus lineatus								X			X			
Trinectes maculatus	X								X					
Spheroides nephelus					X							X		
Chilomycterus schoepfi											X		X	
Totals	15	9	11	19	14	13	16	11	14	17	18	16	20	18

The impoundments were characterized by high densities of several species of atheriniform fishes, as well as the clown goby, Microgobius gulosus, all of which were considered yearly residents. Site I1 showed a slight decrease in total species number during the winter which was quickly made up in the spring, beginning in April. Site I2 did not experience a winter exodus, as did I1. Three of the four seasonally occurring species at I2 were found between October and January. The only commercial or sport fish collected was a solitary Mugil cephalus at site I2 in April.

The yearly residents of the seagrass beds included the atheriniforms and the goby of the impoundments, plus the gulf pipefish, Syngnathus scovelli, and the code goby, Gobiosoma robustum. Juveniles of species of the families Sciaenidae, Gerreidae, and Sparidae were also dominant community members on a more seasonal basis.

The seasonality of both density and energetic standing crop (Tables 18 and 19) at the seagrass sites S1 and S2 and the impoundment site I2 appeared to be on a regular cycle of winter minima and summer maxima. Site I1, in contrast, had three depressions in both density and energetic standing crop, October, March, and June.

The average densities and standing crops of energy at the impounded marsh sites were significantly higher (Student's t, $p < 0.05$) than at the seagrass sites. Differences between the two impoundments and differences between the two seagrass beds were not significant.

The sheepshead minnow, Cyprinodon variegatus, was by far the dominant member of the impoundment communities studied in terms of average density and average standing crop of energy (Table 20). The same atheriniform fish are shared dominants between sites I1 and I2,

Table 18. Total fish densities at each site.

Year & Month	Density (#/m^2)			
	I1	I2	S1	S2
1978 July	22.70	----	5.29	3.37
August	12.59	24.09	0.63	3.76
September	31.56	10.89	2.28	4.57
October	6.10	9.16	2.26	4.00
November	11.48	8.73	1.14	3.98
December	13.61	3.28	0.84	0.90
1979 January	11.23	3.34	2.42	1.64
Februrary	17.65	11.11	2.32	6.81
March	4.36	18.85	1.19	1.06
April	16.20	17.76	1.07	0.82
May	14.25	38.13	2.91	2.00
June	7.09	57.49	4.14	9.40
July	14.88	52.36	10.60	7.94
August	47.19	101.66	13.62	7.32
Mean	16.49	27.45	3.62	7.32

Table 19. Fish standing crops of energy (joules/m^2) at each site.

Year & Month	I1	I2	S1	S2
1978 July	41019	----	17737	9735
August	10147	50072	7642	25949
September	111200	33635	5577	15993
October	8083	49056	8608	9875
November	9318	8846	1093	7933
December	9737	1524	2728	2584
1979 January	19717	5816	4768	6654
Februrary	32538	28034	3746	2996
March	5791	35349	1452	1960
April	133374	31117	2033	1559
May	81034	52791	3614	4156
June	42413	99887	6374	9739
July	87057	103806	14132	9273
August	159985	194279	11637	9713
Mean (all months)	53672	53401	6510	8437
Mean(Sept 78-Aug 79)	58354	53678	5480	6870

Table 20. Percentage of average annual density and standing crop of energy for the major fish species at each site; * = present, but less than 0.2% of average density or less than 0.5% of average standing crop of energy.

Species	Percentage of Average Density				Percentage of Average Standing Crop of Energy			
	I1	I2	S1	S2	I1	I2	S1	S2
Cyprinodon variegatus	80.0	4.6	---	---	87.0	6.7	---	---
Poecilia latipinna	7.4	7.5	---	*	5.9	10.6	---	*
Gambusia affinis	4.2	33.6	---	*	0.6	12.7	---	*
Fundulus grandis	0.02	0.5	---	---	*	6.5	---	---
Menidia beryllina	2.3	0.6	---	*	3.7	1.1	---	*
Menidia peninsulae	2.2	14.9	14.6	20.8	1.5	21.9	33.1	33.8
Lucania parva	3.6	36.1	59.7	58.9	1.3	38.7	27.1	24.3
Microgobius gulosus	0.3	0.6	6.3	4.0	*	1.0	4.9	*
Gobiosoma robustum	---	*	7.3	3.5	---	*	4.1	*
Syngnathus scovelli	*	0.4	5.0	6.9	*	*	*	5.0
Lagodon rhomboides	---	---	0.2	0.4	---	---	11.5	12.0
Bairdiella chrysoura	---	---	1.5	1.4	---	---	4.7	9.3

but I2 has a much more equitable distribution of standing crops of individuals and energy. The two most abundant species across all habitats were the rainwater killifish, Lucania parva, and the silverside, Menidia peninsulae. Within the seagrass beds, the two gobies and the pipefish made up a large fraction of the average number of individuals per month, but, in terms of standing crops of energy, the more seasonal pinfish, Lagodon rhomboides, and silver perch, Bairdiella chrysoura, were much more significant.

Environmental Correlations

The correlations (Spearman Rank) of numbers of fish species, fish density, and fish standing crops of energy to salinity, median water temperature, and standing crops of seagrass (S1 and S2 only) are given in Table 21. The strongest correlations existed between fish standing crops in units of energy and median water temperature, especially at sites I2 and S2.

Correlations of community structure to salinity show a contrasting pattern between the two impoundments. The number of fish species found each month at the low salinity site (I1) was positively correlated with salinity. Site I2 had much higher average salinities and the number of fish species found each month was negatively correlated with salinity. Standing crop of energy, however, had a significant ($\alpha = 0.05$) positive correlation to salinity at I2, while almost no correlation existed between them at site I1. The seagrass beds had no significant correlations between fish community structure and salinity.

Sites S1 and S2 showed contrasting correlations between fish community structure and seagrass standing crop. Site S2 had significant

Table 21. Correlations (Spearman Rank) of structural characteristics of the fish communities at each site with monthly salinity, median water temperature and seagrass density (S1 and S2 only); r = correlation coefficient; Prob > $|r_s|$ with an H_0 of $r_s = 0$; *--significant at $p < 0.05$, **--significant at $p < 0.01$; N = 12.

Site	Structural Characteristic	Salinity		Median Water Temperature		Seagrass Density	
		r_s	Prob > $\|r_s\|$	r_s	Prob > $\|r_s\|$	r_s	Prob > $\|r_s\|$
I1	Number of Fish Species	0.53	0.063	0.65	0.014 *		
	Fish Density	-0.02	0.950	0.40	0.178		
	Fish Standing Crop-Energy	0.07	0.830	0.52	0.066		
I2	Number of Fish Species	-0.40	0.172	-0.48	0.095		
	Fish Density	0.32	0.292	0.70	0.008 **		
	Fish Standing Crop-Energy	0.58	0.038 *	0.83	0.001 **		
S1	Number of Fish Species	0.36	0.220	0.32	0.282	0.11	0.724
	Fish Density	-0.33	0.272	0.33	0.268	0.04	0.887
	Fish Standing Crop-Energy	0.27	0.370	0.59	0.033 **	0.24	0.426
S2	Number of Fish Species	0.20	0.502	0.49	0.090	0.68	0.011 *
	Fish Density	0.15	0.626	0.68	0.011 *	0.45	0.128
	Fish Standing Crop-Energy	0.32	0.294	0.72	0.006 **	0.68	0.011 *

(α = 0.05) positive correlations of species number and standing crop of energy to seagrass standing crop. The correlation of fish density to seagrass was also highly positive, though not significant, at S2. In contrast, site S1 had very weak positive correlations for all three structural characteristics to seagrass standing crop.

Energy Contents

The energy contents of juvenile and adult age classes (Table 22) are significantly site specific (Duncan's Multiple Range Test--"DMRT," α = 0.05). Rather than a continuous gradient of energy content values between the sites, all the sites had significantly different energy contents for juveniles, resulting in a discontinuous gradient of communities. The only overlap of communities was found between the adult fishes in the seagrass beds. The juvenile and adult age classes of the impoundments were not significantly different from each other (DMRT, α = 0.05), but in both cases, as shown in Table 22, were higher in energy content than similar age classes from the seagrass beds. Site S1 was the only site where the two age classes were significantly different in energy content (DMRT, α = 0.05); in that case the average adult had a higher energy content per mg ash-free dry weight than did the average juvenile.

The differences in mean energy content for species at each site are presented in Table 23. Of the two dominants, Menidia peninsulae and Lucania parva, Lucania demonstrated a significantly greater energy content per gram of ash-free dry weight at sites I1, I2, and S2 (DMRT, α = 0.05). The two seasonal dominants in the grassbeds, Lagodon rhomboides and Bairdiella chrysoura, are also significantly

Table 22. Mean energy content of juveniles and adults of all species at each site; means which are not significantly different from each other are connected by a horizontal bar, Duncan's Multiple Range Test, $\alpha = 0.05$.

Juveniles				
N	113	84	111	79
J/mg ash-free dry wt	23.646	23.953	24.743	25.124
Site	S1	S2	I2	I1
Adults				
N	77	82	154	101
J/mg ash-free dry wt	24.086	24.117	24.488	25.299
Site	S2	S1	I2	I1

Table 23a. Mean energy content of common species at site II; means which are not significantly different from each other are connected by a vertical bar, Duncan's Multiple Range Test, $\alpha = 0.05$, N--sample size.

Species	Energy Content (J/mg ash-free dry wt)	N
Lucania parva	25.655	8
Gambusia affinis	25.472	3
Cyprinodon variegatus	25.808	117
Poecilia latipinna	25.052	18
Menidia beryllina	24.839	25
Menidia peninsulae	24.820	20

Table 23b. Mean energy content of common species at site I2; means which are not significantly different from each other are connected by a vertical bar, Duncan's Multiple Range Test, $\alpha = 0.05$, N--sample size.

Species	Energy Content (J/mg ash-free dry wt)	N
Anchoa mitchilli	25.840	4
Gambusia affinis	25.309	49
Lucania parva	25.122	51
Poecilia latipinna	24.804	29
Microgobius gulosus	24.375	11
Menidia beryllina	24.247	15
Cyprinodon variegatus	24.203	42
Fundulus grandis	23.852	30
Menidia peninsulae	23.769	39

Table 23c. Mean energy content of common species at site S1; means which are not significantly different from each other are connected by a vertical bar, Duncan's Multiple Range Test, $\alpha = 0.05$, N--sample size.

Species	Energy Content (J/mg ash-free dry wt)	N
Cyprinodon variegatus	25.531	2
Lagodon rhomboides	24.908	20
Haemulon sciurus	24.277	8
Microgobius gulosus	24.245	18
Gobiosoma robustum	24.221	7
Syngnathus scovelli	23.891	15
Anchoa mitchilli	23.787	5
Leiostomus xanthurus	23.763	3
Eucinostomus (juveniles)	23.756	6
Lucania parva	23.683	36
Oligoplites saurus	23.623	3
Menidia peninsulae	23.598	47
Cynoscion nebulosus	23.303	4
Menidia (juveniles)	23.078	5
Bairdiella chrysoura	22.878	12
Mugil cephalus	22.877	1

Table 23d. Mean energy content of common species at site S2; means which are not significantly different from each other are connected by a vertical bar, Duncan's Multiple Range Test, $\alpha = 0.05$, N--sample size.

Species	Energy Content (J/mg ash-free dry wt)	N
Lucania parva	24.953	53
Lagodon rhomboides	24.758	17
Fundulus grandis	24.539	3
Cyprinodon variegatus	24.249	4
Archosargus probatocephalus	24.173	3
Microgobius gulosus	23.879	9
Menidia peninsulae	23.802	37
Syngnathus scovelli	23.705	21
Floridichthys carpio	23.643	2
Bairdiella chrysoura	23.326	12
Paralichthys albigutta	22.667	3

(DMRT, $\alpha = 0.05$) different in their average energy content per gram of ash-free dry weight in the two grassbeds. Within the impoundments and S2, Cyprinodon variegatus drops to significantly lower energy content per gram of ash-free dry weight than Gambusia affinis and Lucania parva. Also, at I2 the species with higher energy contents appear as more discrete groups than in I1 and S2 and, to some degree, S1.

Fish Community Function

Monthly respiration and production for the major fish species in each community are shown in Tables 24, 25, 26, and 27. Respiration was approximately one order of magnitude greater in the impounded marsh sites (I1 and I2) than in the seagrass sites (S1 and S2). Differences in annual production were even more dramatic, with the impoundments (I1 and I2) roughly 22 and 15 times more productive, respectively, than the seagrass beds.

The impoundment sites were most productive during the months of April and June, whereas the first large pulses of production occurred in the seagrass beds during June and July. All four sites experienced large respiratory losses during July and August. A second staggered seasonal pulse of production was noticeable in the fall, with I1 peaking in September, I2 and S1 delayed until October, and S2 with approximately 39% of its total production occurring during October and November. The bimodal production process of fishes in the seagrass beds is consistent with earlier studies on the shallow water fish communities of the northern Indian River (Schooley 1977) showing a spring/fall recruitment sequence for the shallow seagrass bed communities.

Table 24. Site II respiration and positive production values in J/m^2; R-respiration, P-production, %-percentage of the site's annual total for respiration and production contributed by each species.

Species		Sept 78	Oct	Nov	Dec	Jan 79	Feb	March	April	May	June	July	Aug 79	Totals	%
Cyprinodon variegatus	R	57667	55102	5111	6010	5295	9357	7122	26598	71677	47625	52965	166049	431228	84.2
	P	80038				8180	3659		129069		23942	858		245746	87.3
Gambusia affinis	R	R9	61	37	33	5	3	2	96	424	399	456	4888	6493	1.3
	P	16		38			2				220			276	0.1
Lucania parva	R	15	10	3	2		3	9	56	211	613	3697	6049	10668	2.1
	P			4				5	40		496			545	0.2
Fundulus grandis	R										48	261	219	528	0.1
	P											249		249	0.1
Menidia beryllina	R		192	1207	1388	274	258	438	1392	4516	3389	521	1251	14826	2.9
	P			58	1255	578		382	2182	27494				31949	11.4
Menidia peninsulae	R	1723	1292	965	177	185	171	155	1319	1207	131	132	45	7502	1.5
	P	561		284	125	396						62		1428	0.5
Microgobius gulosus	R	117	205	193	24				26	65	197	422	414	1663	0.3
	P	39	169	151									111	470	0.2
Poecilia latipinna	R	60	21						344	1373	3682	5623	27952	39055	7.6
	P	6									575	112		695	0.2
Symphathus scovelli	R								3	35	14			52	0.01
	P									106				106	0.04
Others	R	144											3	147	0.02
	P														
Totals	R	59815	36883	7516	7634	5759	10422	7726	29834	79508	56098	64077	146870	512142	
	P	80660	169	535	1380	9154	3661	387	131291	27600	25233	1281	111	281462	

Table 25. Site I2 respiration and positive production values in J/m^2; R-respiration, P-production, %-percentage of the site's annual total for respiration and production contributed by each species.

Species		Sept 78	Oct	Nov	Dec	Jan 79	Feb	March	April	May	June	July	Aug 79	Totals	%
Cyprinodon variegatus	R	6006	3145	812	174	15	422	2259	3599	1204	1577	11476	12067	42756	6.5
	P	419					514	834	1089			2483		5339	2.8
Fundulus grandis	R	4819	10538	1956			102	2078	3140	1288	1263	2285	731	28200	4.3
	P	4738	12734						5006		156			22634	11.8
Gambusia affinis	R	3614	1532	1851	1777	310	535	932	2370	8429	16560	24033	40583	102546	15.7
	P		321	1486		160	176	460				1823	2117	6343	3.4
Lucania parva	R	2378	1227	1027	275	169	1171	5221	18545	21533	34597	47526	105736	239405	36.5
	P		317			179	519	2270	22269		11550	7717	10818	55639	29.0
Menidia peninsulae	R	30853	19681	9277	411	203	2178	3255	16510	9230	30678	29496	45	151817	23.2
	P	6799	5128	4627			5363	1243			63000			86160	44.9
Menidia beryllina	R		194	217	19	136	512	328	61		1039	1856	474	4836	0.7
	P			21			329						61	411	0.2
Menidia sp.	R								549					549	0.1
	P								241					241	0.1
Microgobius gulosus	R	818	269	298	116	84	165	327	999	948	433	338	44	4859	0.7
	P		210		215		360	325	1241			149		2500	1.3
Poecilia latipinna	R	5128	4066	1228	404	59	192	625	820	6516	14155	21429	22693	77315	11.8
	P		1666				348	343				9600		11957	6.2
Synanathus scovelli	R	27	123	72	34	23	83	228	529	712	467	30		2328	0.4
	P					40	81			115				236	0.1
Floridichthys carpio	R				47	24	1							72	0.01
	P				90									90	0.05

Table 25. (Extended)

Gobiosoma robustum	R		35	41	2									78	0.01
	P														
Anchoa mitchilli	R							172	287					459	0.1
Totals	R	53683	40810	16779	3259	1023	5361	15425	47409	49860	100769	138469	182373	655220	
	P	11956	20376	6134	305	379	7690	5475	29846	115	74706	21772	12996	191750	

Table 26. Site S1 respiration and positive production values in J/m^2; R-respiration, P-production, %-percentage of the site's annual total for respiration and production contributed by each species.

Species		Sept 78	Oct	Nov	Dec	Jan 79	Feb	March	April	May	June	July	Aug 79	Totals	%
Anchoa mitchilli	R	164	326	88				19	186	131	25	7		946	1.6
	P								296		30			326	2.5
Bairdiella chrysoura	R	203									373	2424	1395	4395	7.3
	P											1945	257	2202	17.0
Cynoscion nebulosus	R	247	260	104							15	33	124	783	1.3
	P		408										78	486	3.8
Haemulon sciurus	R	234									21	23	495	773	1.3
	P														
Lagodon rhomboides	R	1575	744	276								522	581	3698	6.1
	P	1160	906											2066	16.0
Leiostomus xanthurus	R	158					16	15	50	64				303	0.5
	P						111							111	0.9
Lucania parva	R	2253	1843	895	201	24	30	8		764	3707	8083	10598	28406	47.2
	P		61			17	36						89	203	1.6
Menidia peninsulae	R	1612	746	456	91	332	592	396	153	1233	1159	1313	3026	11109	18.5
	P		658		309			372	7		2709	393		4448	34.3
Micropobius gulosus	R	10	15	56	114	245	562	420	434	583	350	56	65	2860	4.8
	P	9		73	118	254	254	96	275		68			1147	8.9
Symphathus scovelli	R	185	177	215	192	180	237	105	105	121	305	426	564	2812	4.7
	P				202	101	59		33	19				414	3.2
Eucinostomus sp.	R		2	16	7	10	9							44	0.07
	P			123		31								154	1.2

Table 26. (Extended)

Hippocampus sp.	R		1	1			8	12	3					25	0.04
	P						25							25	0.2
Brevoortia sp.	R							4	55	196	109			364	0.6
	P									198				198	1.5
Goblosoma robustum	R		4	11	46	107	322	388	503	630	418	344	341	3114	5.2
	P			15		63	152	60	201	374				865	6.7
Others	R		38	34	237	141	4	4				11	93	562	0.9
	P		164		124							2	19	309	2.4
Totals	R	6641	4156	2136	897	1036	1718	1380	1489	3672	6482	13242	17282	60194	
	P	1169	2197	88	876	435	668	528	812	591	2807	2340	443	12954	

Table 27. Site S2 respiration and positive production values in J/m^2; R-respiration, P-production, %-percentage of the site's annual total for respiration and production contributed by each species.

Species		Sept 78	Oct	Nov	Dec	Jan 79	Feb	March	April	May	June	July	Aug 79	Totals	%
Anchoa mitchilli	R	28	1	1			11	32	14					87	0.1
	P							21						21	0.2
Bairdiella chrysoura	R	2181	284								447	2249	1830	6991	8.6
	P	36										1729	426	2191	16.8
Cynoscion nebulosus	R	166	35	1										202	0.2
	P														
Eucinostomus sp.	R	16	17	4	5	2						20	587	651	0.8
	P	13			13							13		39	0.3
Gobiosoma robustum	R	57	109	160	200	92	128	131	93	143	276	187	57	1583	1.9
	P	73		377	19			65	10	91	88			723	5.5
Lagodon rhomboides	R	2098	218	195							32	144	2	2689	3.3
	P														
Lucania parva	R	3139	2401	2495	1020	199	72	18	321	934	6342	7486	6554	30981	38.0
	P		892	776	210	26				406		102	155	2567	19.7
Menidia peninsulae	R	10489	4658	2601	759	493	1053	517	707	505	590	1428	4082	27882	34.2
	P					1117	131		620		37	184		2289	17.5
Microgobius gulosus	R	94	81	169	157	36	110	239	182	987	851	86	46	1058	3.8
	P	117		2859		54	60	484			25			3599	27.6
Opsanus tau	R	149	85									71	75	380	0.5
	P														
Poecilia latipinna	R	16	7											23	0.03
	P	9												9	0.1

Table 27. (Extended)

Syngnathus scovelli	R	394	125	258	246	83	56	97	142	144	1354	1666	655	5220	6.4
	P		70	214		68		90		310	744		113	1609	12.3
Menidia beryllina	R					14	18							32	0.04
	P														
Achirus lineatus	R						27	30		45	52			154	0.2
	P														
Floridichthys carpio	R						12	13				23	24	72	0.1
	P														
Others	R	297	2		156	94	114	125		187	327	86	47	1435	1.8
	P											6		6	0.05
Totals	R	19124	8023	5884	2543	1013	1621	1202	1459	2945	10221	13446	11959	81440	
	P	248	962	4226	242	1265	191	660	630	807	804	2234	694	13053	

Annual production and respiration within site I1 was dominated by Cyprinodon variegatus. The next two dominant species are possibly more noteworthy for their ratio of production to respiration than the absolute quantity of either. Menidia beryllina contributed a disproportionately higher share of production to total community production for its average standing crop and respiratory demands, while the Poecilia latipinna population produced very little net production relative to its large metabolic losses within the system.

At site I2, the impoundment canal, production and respiratory losses were more equitably distributed among six species than they were at I1. The two dominant species were Lucania parva and Menidia peninsulae. The Lucania parva population had a large portion of its annual production in August, as did the Gambusia affinis population. Respectively, they produced 44% and 40% of their yearly population productions during the warm month of August at site I2.

Lucania parva is also a functionally dominant species in the seagrass beds. However, the population's contribution to annual production appears less significant and, at S1, was a minor part of total community production. Two species that were important in their contributions to production within the seagrass beds were Bairdiella chrysoura and Microgobius gulosus. The former was a seasonal recruit from June through September, while the latter was a continual resident of both seagrass beds. The same type of disproportionality in rates of production and respiration found for two populations at site I1 was also found within the seagrass beds. However, in this case it is intraspecific for the species Menidia peninsulae, a dominant functional member of both seagrass beds. Menidia peninsulae made noticeably

different contributions to the annual production and respiratory balance within each community. At site S1 the population's ratio of production to respiration is 0.4, while at site S2 the same ratio is 0.08.

DISCUSSION

Abiotic Factors

The controlling physical factor within the systems studied is the variation in solar radiation. This variation produces a dynamic balance among the influences of direct solar heating, evaporation, and precipitation in generating the daily physical-chemical characteristics of the aquatic habitats studied. During the winter, temperature depression is correlated with reductions in the structure and function of the fish communities.

In the seagrass beds Jones et al. (1975) suggested a two season pattern for the resident fishes. During the warm/wet season they hypothesized an inverse relationship between rainfall, which led to lower salinities, and the number of species occupying the seagrass beds. The second response hypothesized was that during the cold/dry season, even though rainfall was decreasing and salinity rising, the drop in water temperature resulted in a further decline in the number of fish species. Schooley (1977) demonstrated a bimodality in density and diversity in the shallow water habitats of the northern Indian River and Mosquito Lagoon. Because of their shallowness, these habitats may reach zones of appreciable thermal stress during midsummer and midwinter, affecting both residents and seasonal recruits. Both seagrass beds had slight late-summer depressions in density followed by higher levels in the fall.

Within the impoundment I2 the correlations of both salinity and temperature to fish community structural characteristics are unclear due to the influence of marsh morphology. Small changes in water level can have vast surface area effects within the impounded marshes (Snelson 1976). With heavy rainfall, the total marsh area may increase dramatically during the cooler months, as it did at I2 during January. Therefore, subsequent density measurements are lowered as a function of the proximity of newly covered marsh for dispersal of the standing crop. Similarly, during the warmer dry months densities would increase as water evaporated from these shallows. This could lead to a positive correlation of standing crop to salinity. This theory may explain the correlations at I2, but density was not significantly ($\alpha = 0.05$) correlated with mid-channel depth at this site. The significance of this shift in ecological density at I2 remains to be investigated. Similar phenomena are not believed significant at the other three sites.

Day et al. (1973) found temporal patterns within a Louisiana salt marsh and shallow estuarine system to be controlled by temperature, as did Adams (1976a) in a North Carolina Zostera bed. Subrahmanyam and Drake (1975) found no correlation of abundance (numerical or biomass) with seasonal temperatures or salinities in two north Florida salt marshes. However, several species groups did show significant correlations to either temperature or salinity.

The seasonal succession in the recruitment of the juveniles of several species found in earlier studies of seagrass beds (Jones et al. 1975, Schooley 1977) was also observed. This same sort of recruitment sequence, which would be expected for a marsh (Subrahmanyam and Drake

1975), did not, of course, occur within these impounded marshes. Some minor recruitment may occur at water pumping stations (Jack Salmela, personal communication) when water levels are being maintained in the impoundments by the pumping of water in from the open lagoon.

Snelson (1976) concluded that the major factors controlling the spatial distribution of fishes in permanent impoundments were salinity and vegetative cover. Both salinity and vegetative cover differed between the two impoundment sites studies; however, salinity differences between I1 and I2 would not appear to be physiologically significant to the dominant atheriniform fishes. Snelson (1976) and Gilmore (1977) both characterized the impoundments of the Indian River area as stressed environments to which only a small group of species are adapted. During the period of this study the two impoundment sites did not appear any more "stressed" in terms of fluctuations of salinity or temperature than did the shallow seagrass beds. The obvious difference is the open versus closed nature of the two systems. Species within the impoundments do not have a temperature and/or salinity refugium to which they can retreat when conditions become too stressful for that particular species. It appears, then, that knowledge concerning factors other than environmental fluctuations, such as the degree of potential recruitment and the flushing of detritus, may also be important to our understanding of the differences between marsh and seagrass fish communities.

Gilmore (1977) listed 26 species that have been found in the impoundments of the Indian River system. All of them were also found in the open estuary. Snelson (1976) found that brackish impoundments of Merritt Island support about ten species, the dominant six in all

cases being the same that dominated sites I1 and I2. In the grass flats of the Indian River, a total of 208 fish species have been collected (Gilmore 1977), 87% of which are found primarily as juveniles. Approximately 30% of species collected in seagrass beds S1 and S2 were found only as juveniles, and another 21% were found predominantly as juveniles.

The dominant species collected in this study were different than those found to be the dominant grass flat species by Jones et al. (1975). Jones et al. (1975), using a large sweep seine (61 m) to cover an area of 1,161 m^2, described the residents of the grassbeds in the southern portion of the Indian River as being dominated by Eucinostomus gula, Eucinostomus argenteus, Diapterus auratus, Lagodon rhomboides, and Bairdiella chrysoura. The species found to structurally and functionally dominate the seagrass beds in this study were smaller demersal and bottom dwelling forms. The sampling techniques used in this study are biased towards these species, just as the technique used by Jones et al. (1975) was biased against these same species (Gilmore et al. 1976). The techniques used here are assumed to be biased, as are all fish collecting techniques, but are believed to realistically reflect fish standing crops of density and energy within the seagrass beds (Gilmore et al. 1976).

Biotic Factors

The most important biotic factor controlling communities within Indian River seagrass beds is seasonal change in macrophyte standing crop. During the spring and early summer, the grass beds provide greater habitat complexity and strongly influence the physical,

chemical, and biological processes of the entire system. In the fall the grass beds, often carpeted with diatoms, die back, producing vast amounts of detritus that show up about six weeks later with a resulting pulse of organic carbon into the sediment (Clark 1975). This seasonal pulse effect appears to be a general characteristic of seagrass-based ecosystems (Phillips 1960, Odum 1967, and Phillips 1974). Clark (1975) discussed the effects of this seasonality of detrital input on the dominant groups of benthic invertebrates within the lagoon. The density of invertebrates in both seagrass beds, S1 and S2, was greatest in January, followed by July, April, and October, in that order. In Clark's (1975) study of the benthic invertebrate communities of seagrass beds, he found two peaks in density, the maximum peak being in November-December with a second in May. The seagrass beds studied here appear to operate under the same seasonal density patterns as those studied by Clark (1975). The seasonality of detritivores has an overwhelming influence on total benthic invertebrate density in the grass beds of the northern Indian River (Clark 1975). Clark (1975) pointed out that the early winter peak in density is a direct response to that growing-season's decomposing seagrass, while the early summer peak may be a response to increased availability of refractory detritus, which was not decomposable at lower winter temperatures. However, he also pointed out that the reproduction of temperate species is keyed to increasing vernal temperatures and is a factor contributing to the early summer peak in density as well. This sequence of density cycling which is keyed to detrital input and reactivation appears to dynamically link the benthic invertebrate community with the production and seasonal recruitment of fishes within the seagrass beds.

Within the impoundments the pulsing, if any, of detrital input is not known. Pool et al. (1974) reported a general pattern of increased leaf fall during the rainy season for mangrove forests in south Florida. If this is true for the impoundment mangroves of the Mosquito Lagoon area, maximum leaf fall, on the average, would occur during June, July, and August. The maximum standing crops of Chara occurred in December and September at sites I1 and I2, respectively. Based on this limited information, it is speculated that the two primary detrital sources are pulsed, but not synchronously. Mangrove litter is assumed to produce a late summer pulse in finer detrital particles; winter diebacks of Chara, on the other hand, would produce a spring pulse in utilizable organic material as temperature increases speed up bacterial and meiofaunal detrital processing. The seasonality of invertebrate infaunal densities at site I2 appears to correlate with such a model of detrital pulses, since densities in fall and spring are greater than in winter and summer. This is the reverse of what was observed for density in the seagrass beds. The same pattern found for density and energetic standing crop at I2 was also found for standing crop at I1. The density at I2 during the fall was less than that found during the winter. The greater than average rainfall during December may have produced greater litter production during this time. If isopod populations tracked this hypothesized pulse in detritus by increased reproduction, it would explain their numerical dominance and relatively smaller contribution to energy standing crop per individual due to a predominance of juveniles and immature individuals.

The amount of detritus produced in the impoundments appears to be greater than in the seagrass beds. Unfortunately, with complete data

from only one impoundment, the significance of the difference found is not known. Chara, which was found in dense patches in various portions of the impoundments only contributed 20% of estimated net production. The production estimate for the impoundment mangroves of site I1 (0.47 $g \cdot m^{-2} \cdot d^{-1}$) is approximately of the same level as those found for mangrove scrub forests at Turkey Point in southeast Florida (Pool et al. 1974). This forest is then about 25% as productive as basin forests of southern Florida, which have greater freshwater turnover than scrub mangrove forests.

Annual net production in the seagrass beds averaged 3,060 $kJ \cdot m^{-2} \cdot y^{-1}$ for sites S1 and S2. By comparison, using Eiseman et al.'s (1976) estimate of above ground monthly standing crop and applying the same calculations and conversions, an average of 3,065 $kJ \cdot m^{-2} \cdot y^{-1}$ was derived. Clark's (1975) estimate of monthly standing crop for northern Indian River seagrass beds applied to this same formula yielded an estimated average annual net production of only 1,273 $kJ \cdot m^{-2} \cdot y^{-1}$. Red and brown algae, which were not significant in the shallow grassbeds at S1 and S2, did contribute to production in the deeper sites studied by Clark (1975) and Eiseman et al. (1976). Maximum minus minimum standing crop was used as an estimate of net production of algae (Steve Davis, personal communication). Net production was converted to joules based on average calorimetry values for phaeophytes and rhodophytes of 12.79 and 13.27 J/mg dry wt, respectively (Cummins and Wuycheck 1971). This would add 279 $kJ \cdot m^{-2} \cdot y^{-1}$ due to red algae production to the 1,273 $kJ \cdot m^{-2} \cdot y^{-1}$ produced by seagrass in the area studied by Clark (1975). Red algae are estimated to produce 783 $kJ \cdot m^{-2} \cdot y^{-1}$ and brown algae 224 $kJ \cdot m^{-2} \cdot y^{-1}$ for a total of 1,007 $kJ \cdot m^{-2} \cdot y^{-1}$ in the

grassbeds studied by Eiseman et al. (1976). In these two cases, estimates of net seagrass production were 3 to 4.5 times that estimated for large algae.

The seagrass beds of this system are on the lower end of the range of annual production for seagrass-based ecosystems. Assuming 1 gC is equivalent to 42 kJ, production estimates in $kJ \cdot m^{-2} \cdot y^{-1}$ for Zostera beds were 8,943 and 5,280 in North Carolina (Adams 1976b), 24,528 in Puget Sound (Phillips 1974), and, for a Thalassia bed in the Caribbean, up to 122,640 (Thayer et al. 1975b).

Production in both the impoundments and the seagrass beds is very low relative to similar systems. The reduced circulation in mangrove impoundments such as I1 is believed to be partially responsible for lowered mangrove production. The frequency and duration of winter freezes may also be a significant factor. Within the seagrass beds Clark (1975) speculated on four nonexclusive hypotheses for reduced production within the grass beds of the Mosquito Lagoon and northern Indian River. They were

1. lack of appreciable currents, leading to localized depletion of nutrients;
2. nutrient limitation due to sediment characteristics (i.e. coarse sediments with less surface area for microbial regeneration of nutrients);
3. intolerance to low temperatures for seagrasses at the northern extent of their range; and
4. carbonate limitation.

The characteristics of the entire ecosystem and specifically the fish communities are possibly then controlled by these same processes.

Production

Total production in each system was the sum of the positive production values for each species each month. Negative production values were excluded for the summation of total production, which according to Chapman (1978) should be done if one is interested in community metabolism and estimating assimilation and production efficiencies between trophic levels. The most noticeable portion of production not taken directly into account by these calculations is production in the form of reproductive products. This is assumed to have a greater potential impact on underestimating the production at sites I1 and I2 which had a larger percentage of year-round residents than did the seagrass beds. The impact of this omission in the overall production estimates is not known.

Total fish production within the seagrass beds was very similar, 12.95 and 13.05 $kJ \cdot m^{-2} \cdot y^{-1}$. The impoundments had much higher production levels, 281.46 and 191.75 $kJ \cdot m^{-2} \cdot y^{-1}$. The seagrass bed, though similar in overall production levels, were rather dissimilar in the relative contribution to site production by year round residents of the grassbed and seasonal recruits, which were predominantly juveniles. At site S1 the seasonal recruits produced 42% of the yearly total production, whereas at S2 they only contributed 17%. The diurnal resident Anchoa mitchilli accounted for 3% of the yearly production at site S1 while at S2 it contributed approximately 0.1%.

There are few comparative studies of finfish production in marine systems. Clarke (1946), based on commercial landings for George's Banks, estimated a harvest production of 0.15-0.73 g dry $wt \cdot m^{-2} \cdot y^{-1}$.

He estimated net production as possibly twice this, or 0.30-2.46 g dry wt$\cdot m^{-2} \cdot y^{-1}$. Merriman and Warfel (1948) estimated annual production for fishes in Block Island Sound to be 1.1-2.2 g dry wt$\cdot m^{-2} \cdot y^{-1}$. Harvey (1950) found the production for pelagic and demersal fish in the English Channel at approximately 1 g dry wt$\cdot m^{-2} \cdot y^{-1}$; Hellier (1962), at Laguna Madre in Texas, estimated a production of approximately 3.1 g dry wt$\cdot m^{-2} \cdot y^{-1}$ for the four dominant species; Day et al. (1973), for a marsh-estuarine system in Louisiana, estimated production at 21.8 g dry wt$\cdot m^{-2} \cdot y^{-1}$; Adams (1976b), in North Carolina seagrass beds, estimated production at 21.7 kcal$\cdot m^{-2} \cdot y^{-1}$ ($\sim$4.6 g dry wt$\cdot m^{-2} \cdot y^{-1}$).

Assuming 19.85 kJ/g dry wt, the production in the seagrass beds is 0.65 g dry wt$\cdot m^{-2} \cdot y^{-1}$ and in the impoundments 14.8 and 9.66 g dry wt$\cdot m^{-2} \cdot y^{-1}$. Therefore, the impounded marshes and seagrass beds in Mosquito Lagoon are on opposite ends of the range of yearly production found for marine fish communities.

Production in temperate lentic freshwater fishes has ranged up to 40 g dry wt$\cdot m^{-2} \cdot y^{-1}$. In general, highly productive standing fresh waters in temperate regions produce around 15 g dry wt$\cdot m^{-2} \cdot y^{-1}$ (Chapman 1978). Tropical and fertilized systems can produce much higher levels. Some tropical lakes are at maximum equilibrium with yields higher than 10 g dry wt$\cdot m^{-2} \cdot y^{-1}$ (Welcomme 1972). Naiman (1976) reported 155.4 g dry wt$\cdot m^{-2} \cdot y^{-1}$ in Tecopa Bore, a desert stream in Death Valley, California. Lotic ecosystems are capable of sustaining even higher levels than lentic systems. A phenomenal 197 g dry wt$\cdot m^{-2} \cdot y^{-1}$ was produced in 1967 by 10 species of fish in the River Thames (Matthews 1971).

The ratio of production to average biomass can be a useful means of comparing similar aquatic systems as well as providing a general multiplier, which can be considered a secondary productivity function. This function would then allow production to be estimated without measuring more than average biomass (Chapman 1978). The seagrass beds, S1 and S2, had $P/\bar{B}$ ratios of 2.36 and 1.90, respectively. The impounded marsh sites, I1 and I2, had ratios of 5.24 and 3.59, respectively. Mann (1965) hypothesized that communities with $P/\bar{B}$ ratios < 1 were energy limited. If this hypothesis is true, then none of the communities studied would appear to be energy limited. Backiel (1971) found a $P/\bar{B}$ ratio of 0.62 for predatory fish in Poland, Mann (1965) found a value of 0.65 for fishes in the River Thames, and MacKinnon (1973) calculated a ratio for a large slow-growing population of American plaice as 0.4. Subsequent studies on the River Thames have given ratios of 2.85 (Burgis & Dunn 1978). Two large freshwater systems, Lake George, Uganda, and Loch Leven, Scotland, had ratios of 1.43 and 2.13, respectively (Burgis & Dunn 1978).

The $P/\bar{B}$ ratio is also an expression of energy turnover within the fish community. The vast differences in total annual fish production between the seagrass beds and the impoundments are not simply a result of greater average standing crops in the impoundments but also that the impoundment fishes are turning energy over at a faster rate as shown by their respective $P/\bar{B}$ ratios. The faster turnover of I1 compared to I2 is due to the relatively higher turnover rate (5.3) within the Cyprinodon variegatus population at site I1. At site I2 this same species had a turnover rate of 1.6. In comparing the two seagrass beds, site S1 had the higher rate and was also the bed with

the highest percentage of production by the juveniles of seasonal recruits to the grassbeds. Adams (1976b) found ratios of 2.85 and 2.77 for fish in North Carolina seagrass beds. He attributed these high turnovers to production by juveniles which he estimated at 79% and 84% of the total annual production for all species. High juvenile production would also appear to partially explain the very high turnover of 18.6 found by Day et al. (1973) in a productive Louisiana estuary.

Respiration

The seasonality of median water temperature appreciably influenced the balance of production to respiration during the year. The ratios of $R/\bar{B}$ during January at sites I1, I2, S1, and S2 were 0.29, 0.18, 0.22, and 0.15, respectively. During August, the ratios at these same sites were 0.92, 0.94, 1.49, and 1.44, respectively.

The annual respiratory losses at sites I1, I2, S1, and S2 were 512, 655, 60, and 81 $kJ \cdot m^{-2} \cdot y^{-1}$, respectively. The ratios of total annual respiration to average biomass, in the same order, were 8.77, 12.20, 10.94, and 11.79. Day et al. (1973), without compensating for temperature, calculated the same ratio to be 13.16 for fishes in a Louisiana estuary, and Adams (1976b), who did compensate for temperature, reported a ratio of 8.88 for the fishes in a North Carolina seagrass bed. In the shallow-water habitats studied here, standing crops were positively correlated with water temperature. This was also the case in both the Louisiana and North Carolina fish communities. Therefore, the wide range of monthly respiratory energy losses within the fish community results because fish densities are greatest at the

same time higher water temperatures are producing higher rates of metabolism and vice versa.

Consumption

Consumption is a more appropriate indication of the functional significance of the fish community in turning over energy within the aquatic ecosystem than is production per unit area because it includes production and energy losses due to respiration. A classic example of this is the work of Davis and Warren (1965) who studied trophic relationships of cottids in an experimental stream. They found that, to a point, production increased with biomass, but then it began to fall as biomass increased further. Due to the increased interaction of individuals at higher levels of fish biomass, most of the food available was used for maintenance; at lower levels of biomass more of the available food was converted to growth.

The calculated annual consumption of each species at each site is presented in Tables 28, 29, 30, and 31. Total consumption per unit area within the impounded marsh was approximately an order of magnitude higher than that occurring in the seagrass beds. Within the impoundments, Cyprinodon variegatus accounted for 44% of the annual consumption. Lucania parva, Poecilia latipinna, Gambusia affinis, and Menidia peninsulae consumed 19%, 8%, 7%, and 1% of the total, respectively. In the seagrass beds, the majority of the consumption was within the populations of Lucania parva (37%) and Menidia peninsulae (27%). The seasonal recruits to the seagrass beds accounting for the greatest consumption were Bairdiella chrysoura with 9% and Lagodon rhomboides with 6%. Lagodon rhomboides consumed 64% of the total

energy intake in a North Carolina estuarine fish community (Adams 1976b).

The fish communities are estimated to have consumed a total of 992-1,059 $kJ \cdot m^{-2} \cdot y^{-1}$ in the impoundments and 91-118 $kJ \cdot m^{-2} \cdot y^{-1}$ in the seagrass beds. In a highly productive Louisiana estuary, the fish community consumed 1,257 $kJ \cdot m^{-2} \cdot y^{-1}$ (assuming 1 g dry wt = 19.7 kJ) (Day et al. 1973) and in a Bogue Sound seagrass bed approximately 418 $kJ \cdot m^{-2} \cdot y^{-1}$ were consumed by the fishes (Adams 1976b).

System Efficiencies, Turnovers, and Budgets

The ratio of respiration to consumption (R/C) is an index of the efficiency of energy dissipation within a system. The R/C ratio for each community is presented in Tables 28, 29, 30, and 31. The impoundments, I1 and I2, had R/C ratios of 0.52 and 0.62, while the ratios in the seagrass beds, S1 and S2, were 0.66 and 0.69, respectively.

The conditions in the impoundments and seagrass beds seem to span the normal range of conditions found in other fish communities. A ratio of 0.61 was found for fishes in the seagrass beds of Bogue Sound (Adams 1976b), 0.62 for an American plaice population in temperate waters (MacKinnon 1973), 0.67 for a freshwater fish community in Poland (Backiel 1971), and 0.73 for the total fish community in the River Thames (Mann 1965). Day et al. (1973), in computing the energy budget for a Louisiana estuary, assumed an assimilation efficiency of 50%, which is significantly different from the 80% assimilation assumed in this study. Therefore, his R/C of 0.24 is believed to be unrealistically low.

Table 28. Total annual respiration, production, and consumption at site I1.

Species	Respiration (R) $(J \cdot m^{-2} \cdot y^{-1})$	Production (P) $(J \cdot m^{-2} \cdot y^{-1})$	Consumption (C) $(J \cdot m^{-2} \cdot y^{-1})$	P/C	R/C	P/R
Cyprinodon variegatus	431208	245746	846243	0.29	0.51	0.57
Fundulus grandis	528	249	971	0.26	0.54	0.47
Gambusia affinis	6493	276	8461	0.03	0.77	0.04
Lucania parva	10668	545	14016	0.04	0.76	0.05
Menidia beryllina	14826	31949	58469	0.55	0.25	2.15
Menidia peninsulae	7502	1428	11163	0.13	0.67	0.19
Microgobius gulosus	1663	470	2666	0.18	0.62	0.28
Poecilia latipinna	39055	693	49685	0.01	0.79	0.02
Syngnathus scovelli	52	106	198	0.54	0.26	2.04
Others	147	----	184	----	0.80	----
Total Fish Community	512142	281462	992056	0.28	0.52	0.55

Table 29. Total annual respiration, production, and consumption at site I2.

Species	Respiration (R) $(J \cdot m^{-2} \cdot y^{-1})$	Production (P) $(J \cdot m^{-2} \cdot y^{-1})$	Consumption (C) $(J \cdot m^{-2} \cdot y^{-1})$	P/C	R/C	P/R
Anchoa mitchilli	459	----	574	----	0.80	----
Cyprinodon variegatus	42756	5339	60119	0.09	0.71	0.12
Floridichthys carpio	72	90	203	0.44	0.35	1.25
Fundulus grandis	28200	22634	63543	0.36	0.44	0.80
Gambusia affinis	102546	6543	136361	0.05	0.75	0.06
Gobiosoma robustum	78	----	98	----	0.80	----
Lucania parva	239405	55639	368805	0.15	0.65	0.23
Menidia beryllina	4836	411	6559	0.06	0.73	0.08
Menidia peninsulae	151817	86160	297471	0.29	0.51	0.57
Menidia sp.	549	241	988	0.24	0.56	0.44
Microgobius gulosus	4859	2500	9199	0.27	0.53	0.51
Poecilia latipinna	77315	11957	111590	0.11	0.69	0.15
Syngnathus scovelli	2328	236	3205	0.07	0.73	0.10
Total Fish Community	655220	191750	1058715	0.18	0.62	0.29

Table 30. Total annual respiration, production, and consumption at site S1.

Species	Respiration (R) $(J \cdot m^{-2} \cdot y^{-1})$	Production (P) $(J \cdot m^{-2} \cdot y^{-1})$	Consumption (C) $(J \cdot m^{-2} \cdot y^{-1})$	P/C	R/C	P/R
Anchoa mitchilli	946	326	1590	0.21	0.59	0.34
Bairdiella chrysoura	4395	2202	8246	0.27	0.53	0.50
Cynoscion nebulosus	783	486	1586	0.31	0.49	0.62
Eucinostomus sp.	44	154	248	0.62	0.18	3.50
Gobiosoma robustum	3114	865	4974	0.17	0.63	0.28
Haemulon sciurus	773	----	967	----	0.80	----
Hippocampus sp.	25	25	63	0.40	0.40	1.00
Lagodon rhomboides	3698	2066	7205	0.29	0.51	0.56
Leiostomus xanthurus	303	111	518	0.21	0.58	0.37
Lucania parva	28406	203	35761	0.01	0.79	0.01
Menidia peninsulae	11109	4448	19446	0.23	0.57	0.40
Microgobius gulosus	2860	1147	5009	0.23	0.57	0.40
Syngnathus scovelli	2812	414	4033	0.10	0.69	0.15
Brevoortia sp.	364	198	703	0.28	0.52	0.54
Others	562	309	1089	0.28	0.52	0.55
Total Fish Community	60194	12954	91438	0.14	0.66	0.22

Table 31. Total annual respiration, production, and consumption at site S2.

Species	Respiration (R) $(J \cdot m^{-2} \cdot y^{-1})$	Production (P) $(J \cdot m^{-2} \cdot y^{-1})$	Consumption (C) $(J \cdot m^{-2} \cdot y^{-1})$	P/C	R/C	P/R
Anchoa mitchilli	87	21	135	0.16	0.64	0.24
Bairdiella chrysoura	6991	2191	11478	0.19	0.61	0.31
Cynoscion nebulosus	202	----	253	----	0.80	---
Eucinostomus sp.	651	39	863	0.05	0.75	0.06
Floridichthys carpio	72	----	90	----	0.80	----
Gobiosoma robustum	1583	723	2883	0.25	0.55	0.46
Lagodon rhomboides	2689	----	3361	----	0.80	----
Lucania parva	30981	2567	41935	0.06	0.74	0.08
Menidia beryllina	32	----	40	----	0.80	----
Menidia peninsulae	27882	2289	37714	0.06	0.74	0.08
Microgobius gulosus	3058	3599	8321	0.43	0.37	1.18
Opsanus tau	380	----	475	----	0.80	----
Poecilia latipinna	23	9	40	0.23	0.58	0.39
Syngnathus scovelli	5220	1609	8536	0.19	0.61	0.31
Achirus lineatus	154	----	193	----	0.80	----
Others	1435	6	1801	0.003	0.80	0.004
Total Fish Community	81440	13053	118116	0.11	0.69	0.16

In comparing this study's seagrass beds, sites S1 and S2, with the impounded marsh, I1 and I2, the fishes of the impoundments appear to be using less of their consumed energy for metabolic purposes relative to production than the fish communities of the seagrass beds. One possible explanation for this is that the several species of atheriniform fishes that dominate the impoundments are well adapted to the rigors of environmental fluctuations typical for impoundments (Snelson 1976). However, as noted earlier, during this study the impoundments appeared to be subject to less stress, in terms of salinity and temperature, than were the shallow seagrass beds.

Evidence that appears to support the idea that the seagrass beds are indeed physiologically more stressful than the impoundments are the R/C ratios of the two species that occur most frequently in both impounded and seagrass habitats, Lucania parva and Menidia peninsulae. Lucania parva had an average R/C ratio of 0.71 in the impoundments and 0.77 in the seagrass beds. Menidia peninsulae had an R/C ratio of 0.59 in the impoundments and 0.66 in the seagrass beds. In both cases, the seagrass bed population of each species was using more of its consumed energy for metabolic purposes than for growth. Other explanations such as increased search time for prey are possible, and probably are operating, but are not believed to be as significant as physiological stress (Adams 1976a, Cameron 1969). In discussing why the eelgrass fishes of Bogue Sound were apparently apportioning a lower percentage of consumption to respiration, Adams (1976b) discussed the "adaptation to stress" explanation above. Adams also went on to develop a second hypothesis that abundant energy supplies available within the eelgrass systems may be favorable enough to overcompensate

for assumed environmental stress of the eelgrass beds. The response of the fish communities studied here would support an "excess energy-metabolic compensation" hypothesis assuming environmental stresses in the impoundments and seagrass beds to be equal.

A very important energetic ratio for relating two trophic levels is the ratio of production to consumption (P/C); see Tables 28, 29, 30, and 31. This ratio gives the gross production efficiency, also referred to as ecological efficiency by Slobodkin (1960). The gross production efficiencies for the fish communities at sites I1, I2, S1, and S2 were 28%, 18%, 14%, and 11%, respectively. The impounded marsh communities are, therefore, more efficient at converting consumed energy into fish production. The range of gross production efficiencies for the functionally dominant species (consumption > 600 $J \cdot m^{-2} \cdot y^{-1}$) in each community were 1-55% for I1, 5-36% for I2, 1-31% for S1, and 5-43% for S2.

Ricklefs (1979) listed a range of gross production efficiencies for aquatic poikilotherms from 1.5% for stream limpets feeding on algae to 32% for the freshwater fish, Megalops cyprinoides, feeding on fish. Welch (1968) gave a general range of 15-35% for gross production efficiencies in populations of aquatic consumers. For fish communities, a broad range of gross production efficiencies has also been found. Mann (1965) found the fish community of the Thames River to have a gross production efficiency of 6%, with values of 13-14% for young fish and 1-3% for fish over 4 years of age. Fish communities of seagrass beds in Bogue Sound which were dominated by juveniles had gross production efficiencies of 18-22%.

Finally, we can examine the efficiency of transfers of solar energy into net fish production at each site. We can do this by examining the process as two transfers; solar to net primary (or detrital) production and detrital production to net fish production. The average yearly solar input is estimated to be 6,694 x 10^3 $kJ \cdot m^{-2} \cdot y^{-1}$, based on a twelve-year average for Orlando, Florida, 75 km west of Mosquito Lagoon. The efficiency of transfer of incident solar radiation into detrital production at site I1 is 0.064%. This is calculated from 4,306 $kJ \cdot m^{-2} \cdot y^{-1}$ (mangrove and Chara detrital production)/6,694 x 10^3 $kJ \cdot m^{-2} \cdot y^{-1}$ (solar input). The same method of calculation for S1 and S2, using seagrass production, yields transfer efficiencies of 0.036% and 0.055%. Whittaker (1975) stated that efficiencies of 0.91% and 0.066% are representative values of ecosystems of moderately high and relatively low efficiency of capture. Both the impoundments and the seagrass beds can be considered to have low gross production efficiencies.

The transfer of net detrital production into fish production was, at site I1, 6.53% [281 $kJ \cdot m^{-2} \cdot y^{-1}$ (fish production)/4,306 $kJ \cdot m^{-2} \cdot y^{-1}$ (mangrove and Chara detrital production)]; at site S1, 5.39% [130 $kJ \cdot m^{-2} \cdot y^{-1}$ (fish production)/2,413 $kJ \cdot m^{-2} \cdot y^{-1}$ (seagrass net production)]; and, at site S1, 3.53% [131 $kJ \cdot m^{-2} \cdot y^{-1}$ (fish production)/3,707 $kJ \cdot m^{-2} \cdot y^{-1}$ (seagrass production)]. The higher percentages of the predominantly herbivorous Cyprinodon variegatus and Poecilia latipinna in the impounded marsh are partially responsible for higher efficiency in the marsh as compared to the seagrass beds. However, what is most interesting is that while herbivores account for approximately 88% of all fish production at I1 as compared to less than 2% at S1 and S2, the efficiency of I1 is only 22% greater than the more efficient seagrass

bed. Over 87% of the fish production in the impoundment I1 is from direct grazing on detritus while 98% of the production in the seagrass beds is based on feeding done by the secondary consumers, one trophic level higher than the herbivore/detritivores of I1. Therefore, the seagrass bed communities are very efficient, almost twice the biosphere average (Whittaker 1975), at coverting net primary production into production at the secondary consumer level.

The overall efficiency of conversion of incident solar radiation to fish production is an index of ecosystem energetics which includes the effects of factors affecting photosynthesis, consumption, assimilation, respiration, and growth processes at all trophic levels. This index can be used to compare a variety of aquatic systems. This ratio for each community studied here is 0.0042% for I1, 0.0029% for I2, 0.00019% for S1, and 0.00020% for S2.

When the values found for the percentage of total solar energy being fixed and finally converted into fish production are compared to other aquatic systems, the seagrass beds, S1 and S2, are near the median while the impoundments are very high relative to other natural systems. Using the fish production calculated by Adams (1976b) for the seagrass beds of Bogue Sound and assuming a total solar input of $5{,}862 \times 10^3$ $kJ \cdot m^{-2} \cdot y^{-1}$ (Odum 1971:42), the conversion efficiency is 0.0016% of total solar input. Bardach (1959) found a value of 0.0014% for tertiary consumers on a Bermuda reef, Hayne and Ball (1956) calculated an efficiency of 0.0014% for the fish community in a small Michigan pond. Burgis and Dunn (1978) presented efficiencies for Lake George, Uganda, and Loch Leven, Scotland, which when adjusted to total solar input yield efficiencies of 0.00064% and 0.00013%, respectively.

Clarke (1946) estimated an efficiency of conversion of solar radiation into net fish production of 0.00005-0.00025% for the commercially exploited fish of Georges Banks.

As developed earlier, one possible explanation for why the impoundments appear so efficient at converting solar energy to fish production, as compared to the seagrass beds of S1 and S2 and to other aquatic systems, is the higher percentage of production by lower trophic levels in the marsh. In Bardach's (1959) Bermuda reef study, the efficiency calculated of 0.0014% was for fish feeding at two trophic levels above where most of the production took place in the fish community at I1. However, impoundment canal site I2 had most of its production by primary carnivores and is therefore trophically more comparable to more of the references cited than I1. In general, the impoundments are two to three times as efficient as the most efficient system cited. The seagrass beds of Mosquito Lagoon are utilizing solar energy at approximately 5-10% the levels found in the impoundments. The communities in seagrass beds at S1 and S2 are also only 10-15% as efficient in this energy transfer as were the seagrass bed communities in North Carolina (Adams 1976a,b). If we examine this last comparison closely we find that much of the difference in the two seagrass bed systems is due to a much lower efficiency in the transfer of incident solar radiation to net primary production in the Mosquito Lagoon seagrass beds. This efficiency (seagrass production/solar input) was 0.036% at S1 and 0.055% at S2. Adams (1976b) estimated the annual net primary production of the two Zostera beds where his study was done at 5,280 kJ/m^2 and 8,943 kJ/m^2. If we again assume a total solar input of approximately 5,860 x

10^3 kJ•m^{-2}•y^{-1} for the Bogue Sound area, the Zostera beds had efficiencies of 0.09% and 0.15% in converting incident solar energy to net primary production. This is a range of approximately three times that found in the Mosquito Lagoon seagrass beds.

The functional role of the fish communities in the flow of energy within both the marshes and seagrass beds of the Mosquito Lagoon area is significant due to the percentage of net primary production processed by the fish communities. However, the marshes and seagrass beds differ significantly in community structure and the magnitude of their energy flows. A great deal of future research is required within these marshes and seagrass beds to complete the functional comparisons begun here. The areas of highest priority would be to determine the yearly variability in production, the variability in diets of the major species, the degree of internal cycling within the benthic invertebrate and fish communities, the contributions of phytoplankton and zooplankton to energy flow, and the utilization of high marsh after heavy rains.

The rationale for the original impounding in Indian River was to control the hordes of mosquitos that would affect human health and economic development of the area. The benefits from mosquito control achieved by impounding can be put into economic terms with dollar values assigned to the decreased health care costs and increased development brought to the area. The negative aspects of impounding must also be considered. The impact of the complete isolation of high marsh from the lagoon reduces the potential production of commercial and sport fisheries and has a negative impact on these industries. This impact must be translated into economic terms. Then, new cost/benefit ratios can be generated and used to evaluate present and future mosquito control strategies.

Fish Community Summary

1. A total of 44 species of fishes were found in the seagrass beds, 14 of which were also found in the impoundments. No species were found solely in the impounded marsh, and none of the commercial or sport fishes found in the seagrass beds were common in the impoundments.
2. The seagrass bed communities were dramatically different in structure and function from the impounded marsh communities. The dominant trophic levels in the impoundment fish community were the herbivore/detritovores, whereas the seagrass bed fish community was dominated by secondary consumers.
3. The impoundments were dominated by five atheriniform fishes (Cyprinodon variegatus, Poecilia latipinna, Gambusia affinis, Lucania parva, and Menidia peninsulae), and the clown goby, Microgobius gulosus.
4. In the seagrass beds the dominant community residents were Lucania parva, Menidia peninsulae, Microgobius gulosus, Gobiosoma robustum, and Syngnathus scovelli. Important seasonal recruits to the seagrass beds, primarily represented as juveniles, were Lagodon rhomboides and Bairdiella chrysoura.
5. Mean densities of fish in the impounded marsh were 16.5-27.5 (Ind/m^2) while densities in the seagrass beds were only 3.6-7.3 (Ind/m^2).
6. Mean standing crops of fish were 53.7-58.5 kJ/m^2 in the impoundments and 5.6-6.9 kJ/m^2 in the seagrass beds.
7. The number of species, density, and standing crop were used as indicators of structural complexity of the community. At least

one of the three indicators had a significant ($p < 0.05$) positive correlation with the median monthly water temperatures at each site. Only standing crop of fish at site I2 was found to be significantly correlated with salinity. This last correlation is not interpreted as a direct response of the fishes to varying salinities, but actually the result of changing relative densities of fishes as water levels vary in the impoundment, i.e. with increased evaporation, water level drops, salinity goes up, and total marsh surface area decreases.

8. In the seagrass beds the two fish communities had very different responses to seagrass density. At site S1, community complexity showed almost no correlation to seagrass density, while at site S2, increasing complexity was significantly correlated with greater seagrass density.

9. The annual fish production estimates for sites I1, I2, S1, and S2 were 281.46, 191.75, 12.95, and 13.05 $kJ \cdot m^{-2} \cdot y^{-1}$, respectively. Relative to other fish communities, the impoundments are extremely productive and the seagrass beds are only moderate.

10. Over 87% of the fish production at I1 was by herbivorous/detritivorous fishes, whereas fish production of the other sites was primarily by secondary consumers. The conversion of solar energy into fish production at I1 involved one less transfer than is common for many temperate fish communities.

11. The ratios of annual production to average standing crop appear to indicate that the fishes in either habitat are not energy limited and that the fish community of the impoundment has a turnover rate of approximately twice that of the seagrass bed community.

12. Annual respiratory losses at I1, I2, S1, and S2 were 512, 655, 60, and 81 $kJ \cdot m^{-2} \cdot y^{-1}$, respectively. Community respiration was greatest during the summer as a result of higher densities and higher water temperatures.

13. Annual consumption by the impounded marsh fishes was estimated to be an order of magnitude greater per unit area than the fishes of the seagrass beds. Consumption in the impoundments, I1-I2, was 992-1059 $kJ \cdot m^{-2} \cdot y^{-1}$ and in the seagrass beds, S1-S2, was 91-118 $kJ \cdot m^{-2} \cdot y^{-1}$.

14. In comparing the ratios of production to consumption, the impoundment community appears to be more efficient at converting consumed energy into net fish production than the seagrass bed community. Stated another way, the seagrass bed communities use greater percentages of consumed energy for respiratory and maintenance purposes than do the impoundment communities.

15. The overall efficiency of conversion of incident solar radiation into fish production was 0.0042% for I1, 0.0029% for I2, 0.00019% for S1, and 0.00020% for S2. The efficiency of I1 should be viewed with caution since most of the fish production was by herbivores/detritivores as opposed to secondary and tertiary consumers. Production in temperate fish communities is generally by fishes feeding as secondary and tertiary consumers.

16. The efficiency of seagrass bed systems at converting solar energy into fish production is relatively low for shallow water systems due to the low efficiency of transfer of incident solar energy into net seagrass production. The former is

more comparable to efficiencies of continental-shelf and large lake communities.

17. Impoundment I1 had a very high efficiency of transfer of solar energy into fish production, partially as a consequence of the high percentage of herbivorous/detritivorous fishes. Site I2 was more characteristic of temperate fish communities, with most of its production by secondary consumers. Site I2 was only 70% as efficient as I1, but is still highly efficient for temperate fish communities in general.

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BIOGRAPHICAL SKETCH

James K. Schooley was born on November 8, 1951, in Tulsa, Oklahoma. He began his undergraduate studies at the United States Coast Guard Academy in New London, Connecticut. His undergraduate studies were completed at Florida Institute of Technology in Melbourne, Florida, where he graduated summa cum laude in 1975, with a B.S. in oceanography. He received his M.S. in 1977 from the Department of Zoology at the University of Florida. After receiving his Ph.D he will join the faculty at California State University at Hayward.

In the summer of 1973, he was married to the former Kathryn Anne Heckenkemper, also of Tulsa, who is a CPA with Peat, Marwick, Mitchell and Co.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Frank G. Nordlie, Chairman
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Carter R. Gilbert
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Stephen A. Bloom
Assistant Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Jerome V. Shireman
Professor, Forest Resources
and Conservation

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

December 1980

Dean, Graduate School